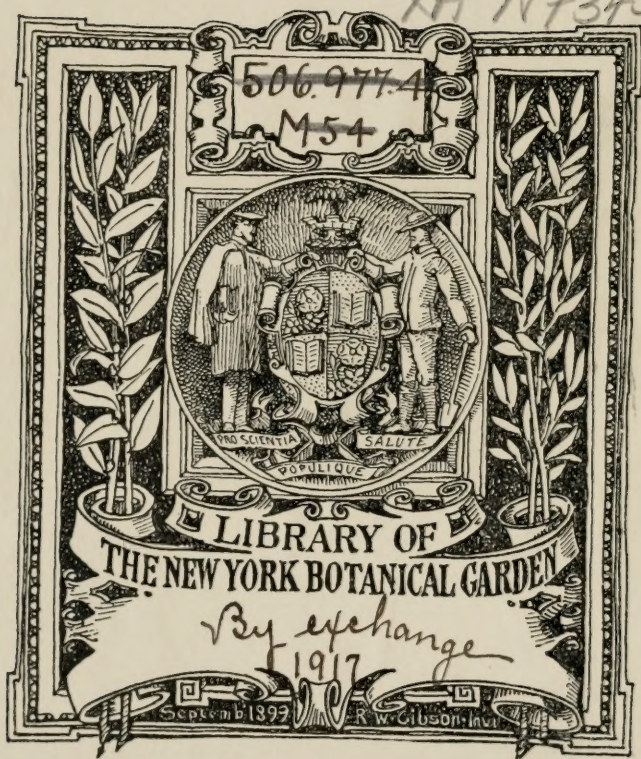


XA
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EIGHTEENTH REPORT
MICHIGAN ACADEMY
OF SCIENCE

1916

XA N7345



EIGHTEENTH ANNUAL REPORT

OF

THE MICHIGAN ACADEMY OF SCIENCE

PREPARED UNDER THE DIRECTION
OF THE COUNCIL

BY

RICHARD A. SMITH

EDITOR

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LANSING, MICHIGAN
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1916.

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LETTER OF TRANSMITTAL.

TO HON. WOODBRIDGE N. FERRIS, *Governor of the State of Michigan:*

SIR—I have the honor to submit herewith the XVIIIth Annual Report of the Michigan Academy of Science for publication, in accordance with Section 14 of Act No. 44 of the Public Acts of the Legislature of 1899.

Respectfully,

RICHARD DE ZEEUW,

Secretary.

East Lansing, Michigan, November, 1916.

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OFFICERS FOR 1916-1917.

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The Council consists of the above-named officers and all resident Past-Presidents.

TWENTY-FIRST ANNUAL MEETING OF THE
MICHIGAN ACADEMY OF SCIENCE.

ANN ARBOR, MICHIGAN

March 28 to 31, 1916.

GENERAL PROGRAM.

Tuesday, March 28

- 4:00 p. m. Council meeting. Room Z 231, Natural Science Building. Reports of committees.
- 4:30 p. m. General meeting of the Academy, Auditorium, Natural Science Building. Election of members.
- 8:00 p. m. Public lecture by Dr. Charles B. Davenport, Director of the Station for Experimental Evolution, Carnegie Institution of Washington, on "The Relation of Juvenile Promise to Adult Performance." Auditorium, Natural Science Building.
- 9:00 p. m. Smoker, given by the Research Club in Alumni Memorial Hall.

Wednesday, March 29

- 8:30 a. m. Council meeting, Room Z 231, Natural Science Building.
- 9:00 a. m. Meeting of sections as follows:
Geology, Room Z 355, Natural Science Building.
Sanitary Science, Upper Lecture Room, New Medical Building.
Botany, Room B 207, Natural Science Building.
Geography and Geology, Room G 217, Natural Science Building.
Economics, Second Floor, Economics Building.
- 1:30 p. m. Meetings of sections for the reading of papers and election of vice-presidents.
- 8:00 p. m. Presidential Address by Prof. Ernst A. Bessey, "The Sexual Cycle in Plants." Auditorium, Natural Science Building. Lecture open to the public.
- 9:00 p. m. General informal social gathering. Room M 333, Natural Science Building.

Thursday, March 30

- 8:30 a. m. Council meeting, Room Z 231, Natural Science Building.
- 9:30 a. m. General business meeting, Room Z 355, Natural Science Building.
- 10:00 a. m. Meeting of sections which have not completed the reading of papers.
- 12:00 a. m. Luncheon for biologists, Room B 100, Natural Science Building.

Friday, March 31

8:00 p. m. Public address under the auspices of the Department of Geology by Dr. Ellen Churchill Semple on "Geographic Influence in Japan," Auditorium, Natural Science Building.

SECTION OF GEOLOGY AND GEOGRAPHY.

I. D. Scott, Chairman

Room G 217, Natural Science Building

Wednesday, March 29, 9 a. m. and 1:30 p. m.

A Conception of Paleogeography. E. C. Case.
 The Extremes of Mountain Glacial Erosion. W. H. Hobbs.
 Underground Water Conditions at the Steere Farm. Frank Leverett.
 Observations on Certain Paleozoic Corals in the Rominger Collection. G. M. Ehlers.
 Pre-Agassiz Glacial Lake in Northern Minnesota. Frank Leverett.
 The Crystallography of Anglesite from the Tintic District, Utah. E. H. Kraus and A. B. Peck.

SECTION OF SANITARY AND MEDICAL SCIENCE.

E. T. Hallman, Chairman

West Lecture Room, Medical Building

Wednesday March 29, 1:30 p. m.

Further studies on the Protein Poison. Dr. V. C. Vaughan.
 Bacterial Study of the Drinking Fountain. Miss Zoe Northrup.
 The Bacterial Flora of the Generative Organs of Cattle. Dr. Ward Giltner.
 Is Bacterium Abortus (Bang) Pathogenic to Humans? L. H. Cooledge.
 The Use of Amniotic Fluid as a Culture Medium. L. C. Ludlum.
 Title to be announced. Dr. F. G. Novy.
 Title to be announced. Dr. P. H. DeKriuf.
 Viability of *Ps. radiceicola* under Aerobic and Partial Anaerobic Conditions. L. O. Ockerblad.
 The Effect of Natural and Modified Soil Conditions on Bacteria. Oswald M. Gruzit.

SECTION OF ECONOMICS.

F. T. Carlton Chairman

Second Floor, Economics Building

Wednesday, March 29, 9:00 a. m. and 1:30 p. m.

The Aldrich-Vreeland Currency and the European War Crisis. George W. Dowrie, University of Michigan.

- Farm Accounting: a Business Problem. C. S. Dunford, Michigan Agricultural College.
- Influences of the Industrial and Social Revolution upon the Agricultural Industry of America. Roy H. Holmes, Hillsdale College.
- The Teaching of Sociology, Its Place in the College Curriculum. G. S. Dow, Olivet.
- Farm Finance. W. O. Hedrick, Michigan Agricultural College.
- Municipal Accounts of Dayton. Frank F. Kolbe, University of Michigan.
- The Valuation of Land. Floyd E. Armstrong, University of Michigan.
- The Teaching of Statistics. Warren S. Thompson, University of Michigan.
- English Taxation. Rufus S. Tucker, University of Michigan.

SECTION OF BOTANY.

LeRoy H. Harvey, Chairman

Room B 207, Natural Science Building

Wednesday, March 29, 9:00 a. m. and 1:30 p. m.

- Reproduction in *Opuntia rafinesquii* (Illus.) Wm. E. Praeger.
- The Hormone Theory of Chromosome Action. (Illus.) Ernst A. Bessey.
- Fern Notes. O. A. Farwell.
- A Convenient Method of Washing Fixed Preparations. Richard de Zeeuw.
- A Macrosporium Disease of Red Clover. (Illus.) L. J. Krakover.
- On the Pronunciation of Scientific Names. H. A. Gleason.
- Some Studies of the Botrytis Neck Rot of Onion. M. T. Munn.
- Pathophytes and Pharmacophytology. A. D. Bush.
- Plants of Chippewa County. (By title.) C. K. Dodge.
- Plants of Schoolcraft County. (By title.) C. K. Dodge.
- Influence of an Incomplete Culture Solution on Photosynthesis. O. M. Gruzit.
- A Simplification of the Present Freezing-Point Method for the Determination of Osmotic Pressure of Plant Saps. O. E. Harrington.
- Further Studies on a Simplified Method for Determining the Conductivity of Electrolytes. (Illus.) R. P. Hibbard.
- Phytophthora infestans in its Relation to Weather. (Illus.) G. H. Coons.
- Smuts of Michigan Plants. (Illus.) G. H. Coons.
- Unreported Michigan Fungi for 1915. (By title.) C. H. Kauffman.
- Some Mycological Features of the Mountains of Washington. (Illus.) C. H. Kauffman.
- The Mucors in Culture and Herbarium. (Illus.) Alfred H. W. Povah.
- The Wintering of *Coleosporium solidaginis*. E. B. Mains.
- The Elementary Species of *Oenothera*; Their Origin by Mutation and Behavior on Hybridization. H. H. Bartlett.
- The Effect of Light, Temperature and Length upon the Geotropic Reaction of Primary Roots. Richard M. Holman.
- The Ferns and Their Distribution about Douglas Lake, Michigan. Frank T. McFarland. Read by H. A. Gleason.

SECTION OF ZOOLOGY.

W. W. Newcomb, Chairman

Room Z 355, Natural Science Building

Wednesday, March 29, 9:00 a. m. and 1:30 p. m.

The Collection of Formicidae in the Museum of Zoology, University of Michigan.

Frederick M. Gaige.

A Synopsis of the Tadpoles of Michigan Frogs. Helen Thompson Gaige.

A New Michigan Turtle. Alexander G. Ruthven.

Fox's List of Michigan Birds. Bradshaw H. Swales.

On the Number of Young in the Garter-snakes. Crystal Thompson.

The Birds of the Douglas Lake Region, Michigan. Norman A. Wood.

A Fossil Musk Ox Skull from Michigan. E. C. Case.

The Rearing of Volvox in the Laboratory. George R. Larue.

Differential Mitoses in the Ovaries of a Gyrinid Beetle. C. P. Russell.

The Origin of Differentiation in the Eggs of Certain Insects. R. W. Hegner.

Periodical Zoological Literature in the Library of the University of Michigan. R. W. Hegner.

Polyembryony in a Parasitic Hymenopteron. R. W. Hegner.

Methods for the Collection and Preservation of Animal Parasitic Worms. George R. LaRue.

The Crane Flies of the Upper Peninsula. J. Speed Rogers.

A Preliminary Survey of the Fauna of Third Sister Lake. J. Speed Rogers.

Oxygen Favoring Male-production in Rotifers. A. Franklin Shull and Sonia Ladoff.

A Problem in Evolution. Bryant Walker.

The Process of Ovulation in Amphibia. Bertram G. Smith.

Notes on Pleodorina californica Shaw. Bertram G. Smith.

Exhibit of Photographs of Michigan Animals. A. F. Combs.

Some Conceptions of Palaeogeography. E. C. Case.

The Phylogenetic Position of the American Opossum. E. D. Huntington.

Some Effects of Sunlight on Paramoecium. H. M. McCurdy.

The Opportunities for Zoological Work at the Biological Station of the University of Michigan. O. C. Glaser.

ECONOMICS.

AN AGRICULTURAL BUSINESS PROBLEM.

BY CHARLES S. DUNFORD.

I.

The agitation for farm accounting in connection with progressive agriculture is not a recent propaganda. Experimental methods applied to agricultural production in the first half of the eighteenth century induced Arthur Young to write, "If this noble spirit continues, we shall soon see husbandry in perfection, and built upon as just and philosophical principles as the art of medicine." In the latter part of this century, however, he complains, "One can not get the farmers to keep accounts." Much experimental effort was expended by husbandmen during the eighteenth century which resulted in an increase in the average yield per acre; at the same time, accounting practice seems to have been neglected. The implication in Arthur Young's conviction of the necessity for the keeping of accounts in connection with the agricultural empiricism of this period is that, in the end, agriculture as a business can not be really scientifically conducted without the keeping of records from which may be deduced certain facts and upon the basis of which information a better reorganization of the production factors may be made.

However, anomalous it may seem, very careful records of the farm business were kept during the thirteenth and fourteenth centuries by English husbandmen. Referring to the latter part of the thirteenth century, J. E. Thorold Rogers in his *Economic Interpretation of History* says, "Nothing can be more carefully and exhaustively drawn than the bailiff's account. He made rough notes of his receipts and expenditures and from the notes, which occasionally survived, the audit was based and the roll engrossed. * * * * * Everything is accounted for, all receipts, including those from the manor court, all rents and all produce. The acreage sown, the seed required for the purpose, the live and dead stock on the farm are carefully noted even to an egg, a peck of tail corn or a chicken, all losses given, all allowances recorded and the audit completed." According to Professor Rogers, these ac-

counts were almost always in Latin and seemed for the most part, to have been the work of the mendicant clergy. These crude single entry records made possible the determination of the approximate gain or loss upon the business of the year.

From the standpoint of agricultural production, the characteristic difference between the periods of the thirteenth and the fourteenth centuries and of the eighteenth century is in the state of the agricultural arts, the prevailing condition in the former being static and in the latter dynamic. Under the static condition of agricultural arts the husbandman felt the pinch of the Law of Diminishing Returns. The exigency of his position impelled a careful analysis of his business. The fairly exhaustive records kept by him attest the premeditated extension of his productive activity. On the other hand, by reason of the progress in agricultural practices during the eighteenth century, less imperative demands were made upon the husbandman for the careful utilization of his productive instruments. The advance in agricultural technique together with the opening for cultivation of large fertile tracts of land in all parts of the world in the period following the Industrial Revolution, outstripped the accumulation of agricultural capital. From a business standpoint this condition freed the agriculturalists of the nineteenth century, in general, from the demands made upon those of the fourteenth century by minimizing the pressure of the Industrial Law of Diminishing Returns.

It is not here implied that during an advance in agricultural practices accounts are unnecessary, for certainly a wiser use of productive factors may be made if it be known what expenditures are more profitable and what are less profitable. The keeping of simple accounts in the industrial stage of increasing returns is advisable. Many losses in labor income could have been averted after the entire rent had been sapped by the extension of productive activity to the better grades of land had the simplest kind of accounts been kept by those occupying marginal land. These accounts certainly would have averted some of the poverty of many communities by inducing a redirection of the productive energies during the plastic period of the husbandman's life.

The first half of the second decade of the twentieth century marks the beginning of a period of a comparatively static condition in agricultural arts. Also, practically all of the better grades of land are now utilized. In these respects the present century, at least temporarily, is similar to the thirteenth and fourteenth cen-

turies. Present day husbandmen, in general, must reckon with the business side of their productive enterprises.

II.

The financial status of any business may be determined by taking an inventory at the beginning and at the end of the year; the gain or loss may then be determined by the difference between the net assets of these two periods. Without this inventory method, annual losses of labor income, interest on investment, and tangible assets may be overlooked. Particularly is this true of the farming business, since a considerable part of the living comes directly from the farm. Thus the farmer may be getting the necessities of life at the expense of his capital without immediately being cognizant of it.

The farming class, however, is not the only derelict group of producers from a business standpoint. Only a few of the 22,000 mercantile and manufacturing establishments that failed last year had an adequate system of accounts. Out of 66,000 concerns doing a business of over \$100,000 each last year, according to Mr. Edward N. Hurley, vice-chairman of the Federal Trade Commission, 30,000 failed to charge off directly anything for depreciation.¹ Thus, they arbitrarily marketed their goods at cut-throat prices.

While the farmer's competition, for the most part, does not take the form of an arbitrary quoting of prices, yet, through a misinterpretation of results attained, or more especially because of a lack of records for the determination of specific costs, his productive effort maybe extended toward increasing the supply of an already unprofitable market. The unprofitableness of this action is further increased by reason of the relative inelasticity of the demand for many of his products.

Farm products, in general, are selling today below marginal cost of production, assuming a reasonable cycle of productive activity, if the wages of the operator be measured by tenant's wages. Farms are being operated in many parts of the United States that give little or no labor income and some are not even paying a reasonable rate of return on the investment. If the farm business be conducted for profit and not for pleasure, an actual known loss *would* certainly suffice to curtail the output. Of course, the so-called unearned increment is, in many instances, a conscious compensating element of advantage which tends to offset the relatively low labor

¹An Address before the Annual Meeting of the Rubber Club of America, at the Waldorf Hotel, New York City, Feb. 2, 1916.

income. Allowing for this and other compensating advantages, nevertheless, owners do continue to operate farms from year to year at an actual unconscious loss of labor income. These annual losses are due to a misinterpretation of results. To some of those who have no system of farm accounts, success is measured by the size of the cash balance at the end of the year. In reality whether or not the degree of success is in direct proportion to the size of the cash balance depends on the nature of the farm enterprise. Where the farm produce consists of cash crops only, success may be so measured. Those engaged in diversified farming, however, who are imbued with this mercantilistic notion are apt either to over-estimate or under-estimate the degree of success with a greater probability of over-estimation as their efforts will be directed towards securing a large cash balance to the detriment of upkeep and assets.

This fact of actual loss is clearly proved by the results of investigations conducted by the Office of Farm Management of the U. S. Department of Agriculture.¹ While these results have been questioned by some due to the fact that much of the necessary information was given to investigators by the farmers from memory, yet accurate accounts kept by many of the farmers indicate that on the whole the figures are fairly reliable. This method of determining profit or loss by the difference between the net assets of two periods respectively furnishes but little useful information, however, that will lead to a better reorganization of the productive factors. By an analysis and comparison of the results of several farms in a given locality, some chance benefit may be derived. Yet, there is nothing in this method to indicate in what departments of the farm showing large gains, those gains have been made. Chance and rule of thumb methods must be displaced by a system of accounts which will serve to furnish such information as will enable the farmer to push vigorously the paying enterprise or to stop an unwarranted expenditure.

III.

The straight single entry or double entry system of bookkeeping such as may be used by a mercantile or manufacturing establishment is neither particularly serviceable nor essential to a farm business. The buying and selling operations which make up most

¹Note: Figures Compiled by the States' Relation Service of the U. S. Department of Agriculture for use in Farm Management Demonstrations during 1915, show that two fifths of 3414 farms investigated indiscriminately in 17 different states, including N. Y., Mich., Neb., Mo., etc., incurred an average loss of labor income.

of the items of the city business are comparatively few in a farm business. Credit accounts are likewise comparatively few. It is not my purpose here to discourage the keeping of detailed records of receipts and expenditures. In fact, it is only by beginning in this matter that the ideal in farm accounting may be attained. But after all, the information acquired by such a system is no more serviceable, in so far as making possible a better organization among the factors of production is concerned, than that obtained by the inventory method.

For accurate information regarding the status of the business which will prevent a misdirection of production, a cost accounting system is essential. Costing systems necessarily involve double entry principles. Two entries must be made for each transaction. If milk be fed to hogs, the dairy must be credited and the hogs charged with the amount, if labor be paid in kind, farm produce must be credited and labor debited, etc. Expediency demands, however, that the system be simplified. Accuracy must be foregone. The tediousness of the trial balance which is indicative of accuracy in posting, suffices to stifle the desire for scientific information of the most enthusiastic farmer. Cost finding requires detailed analysis of the business operations. The many accounts required to furnish the necessary information and the many entries to the various accounts are apt to multiply the adversities of the average farmer beyond the 'elastic limit' of his endurance. In the simplification, posting may be reduced to a minimum by making the entries immediately in the respective ledger accounts. Time cards may be used for the original entries of man labor and horse labor; at the end of the month, the separate items may be posted to their respective ledger accounts and the total hours credited to the ledger accounts of man labor and horse labor. Accounts with the relatively unimportant departments may be dispensed with; the elimination of the cash account saves considerable time and is not particularly essential in the determination of costs. To simplify by eliminating some accounts, and by abandoning the trial balance is to court error but the results will be sufficiently correct for all practical purposes. It must be remembered that the farmer is not producing on contract and in view of this fact, absolute accuracy is not so essential as in the case of the shipbuilder or steel products manufacturer, etc. The vital thing from the standpoint of the propagandist, at least, is to induce the farmer to departmentize his farm and to make an effort to determine what is and what is not profitable. By the use of a simpli-

fied cost finding system, he will be able to determine in connection with his dairy, for instance, whether it is more profitable to sell whole milk or to sell the cream and use skim milk for feeding hogs or calves or poultry.

The principles of cost finding on the farm are in reality no different from those in the factory, i. e., the underlying theory of cost finding is the same. Any system of cost accounting requires, (1) an accurate determination of direct wages paid, (2) an accurate determination of materials used and (3) an apportionment of the indirect expense over the entire products. Practically all of the labor on the farm is direct i. e., specifically applied to a certain job or process. The labor of the farm superintendent is indirect or as sometimes referred to in accounting practice non-productive—which term is, however, inconsistent with Economic terminology—and must be closed into the indirect expense account or allocated separately to the various farm enterprises.

Horse hours and machine hours are also all items of direct charge. By separate accounts with each of the several kinds of farm machinery according to purpose or use, a more exact estimation of costs may be made, e. g., the keeping of a separate account with highly specialized and expensive machinery such as a corn harvester is advisable. Otherwise directly charging the various departments from a single account kept with machinery and equipment, upon the basis of horse hours would give certain inaccurate results, as the cost of the crops requiring the expensive machinery may be underestimated and the costs of others overestimated.

The materials expense, consisting of such items as fertilizers, seeds, etc., presents few difficulties. This year's fertilizing must be apportioned to the several crops succeeding depending on its lasting qualities. The accountant must rely upon the agriculturist for this information.

The farm or indirect expense items such as indirect labor, sundries, taxes, insurance, depreciation on buildings, etc., are proportionately charged to the several departments.

A logical and intelligent interpretation of the results obtained by this method is quite as essential as the results themselves, for an unwise interpretation may nullify the effort put forth. Whether it is more profitable to pasture a woodlot or to cultivate for a crop between the rows of an orchard can only be determined by a comparison of the results with woodlots and orchards under exactly similar conditions that are not pastured or cultivated. That a certain crop pays for all expenses including the expenses of the

orchard is no evidence that the practice of double cropping is more profitable. It is possible that the crop alone or the orchard yield without the cultivated crop would have given a greater return than the double crop, in spite of the fact that with the double crop, the orchard yield seemed to have been pure velvet. Furthermore, no particular year can be assumed to be an average year. Returns in many departments can be estimated only upon the basis of returns for a series of years.

A step toward the inclusion of cost accounting as an element in scientific agriculture, may be made by requiring that all county agricultural agents be trained in the principles of accounting. It is of course essential to teach improved cultural methods but the advice given will result in a more profitable expenditure if it be based upon the study of scientifically determined costs. It is not sufficient to know how to raise more; what to raise under conditions that effect cost on the particular farm and how to market the product most profitably are likewise important. The function of the agriculturist expert obviously is not minimized by the introduction of costing systems; even tho hay be found to be a profitable crop, its perpetual cropping would be inconsistent with scientific agriculture. By minimizing guesswork, on the other hand, farmers may be brought even into closer touch with scientific cultural methods.

The fact is that the individual farmer's business problems are uppermost today. The principles of costing and the principles of marketing are vital both from the standpoint of the farmer and the consuming public. Also, the farmers's commercial credit problems would not be half so difficult of solution if lenders had confidence in his ability to reckon costs, and knew that he did so. That his shortcomings in general along this line may be corrected is evidenced by the successful keeping of a simplified system of costs by many farmers at the present time.¹

Department of Economics,

Michigan Agricultural College, East Lansing.

¹Cf P. 2 U. S. Dept. of Agriculture, Farmers' Bulletin No. 572.

SOME ASPECTS OF MUNICIPAL ACCOUNTING.

BY FRANK F. KOLBE.

A few years ago there was no city in the country whose financial records had been so systematized as to furnish the information necessary for the exercise of administrative judgment and proper control. Private business was keeping its accounts in such a manner that at regular intervals it was able to furnish its owners and managers with two statements—one, showing the assets and liabilities of the business; the other, the revenues for the period and the expense or cost of getting those revenues. The first statement, that of assets and liabilities, shows the stockholder whether his investment in the business is being maintained and whether his net assets are increasing or decreasing, and the forms which that investment is taking—whether in quick assets like cash, accounts receivable, or finished goods or in fixed assets like plant and machinery.

While the same importance does not attach to a balance sheet for a public corporation as for a private one, such in the case of a city would show several things of importance. Thus, it would indicate clearly whether the city is making proper provision for the payment of its debts. It is a common thing for a city to borrow money to build pavements. At the beginning it will have the pavement in its property accounts and the debt owned in its liability accounts. At the end of the life of the pavement it will be taken out of the property accounts and if the debt is not extinguished but refunded, such improper financing will show itself in the increasing percentage of debts to property. Debts incurred to pay current deficits will show up in the same manner. In Dayton in 1907, the city ran behind some \$150,000 which it paid by a bond issue running for fifteen years. The years previous to 1922 in which the sinking fund is accumulated to pay these bonds will have to bear the expenses of cleaning the streets and furnishing fire and water protection to the citizens of 1907 and also the interest thereon. Furthermore, a statement of property owned is the first step in fixing responsibility for that property. It is impossible to hold anyone responsible for anything unless you know what has been intrusted to him. Such a statement contains also the amount of the sinking fund assets accumulated to retire the bonded debt.

A comparison of these amounts with the amount that should be in the sinking fund as determined by accurate computation will show whether the administration is putting the proper amount of money received from taxation into the sinking fund or whether it is spending it on current operation. An administration may thus shift the cost of the services which it furnishes to future taxpayers by funding its operating expense or not making the proper provision for the retirement of its bonded debt. If a pavement is expected to last fifteen years, one-fifteenth of the cost (approximately) should be placed in a sinking fund each year—not leaving it for the last year of the fifteen or for years after that to provide the money with which to retire the bonds and thereby pay for the pavement used by previous taxpayers. Any statement which will show the shifting of burdens to periods other than those in which the service is received is a valuable one.

Nor is the usefulness of the property and liability accounts confined to giving general information concerning the collective results of the period. Such accounts are supported by detailed schedules so that if anyone wants to know, for instance, to whom the city owes a certain bill and how long it has owed it, the record is immediately accessible. Any good system of accounting is so arranged that all debts not paid within a reasonable time after delivery of the goods or services are automatically brought to the attention of the proper official. This will assure that the city will always get the two per cent discount offered for prompt payment. This assures also that there shall be no discrimination between sellers to the city by holding up payments to some for months and paying others immediately. It is not claimed that a good accounting system will prevent discrimination or assure a business-like administration but it will assure that the same information and statistical aid will be at hand for the management of public business as are at present available for private business. It will also provide for holding someone definitely responsible for everything that is done. A statement of property and liabilities shows the newcomer his heritage of property as well as his heritage of debt. Ordinarily only the second is furnished him and sometimes not even that.

The second statement used by private business is the revenue and expense statement. It is often assumed that its principal function is to furnish a statement of profits earned. If this were its only function, it would be superfluous, for profits can be determined from the first statement by finding the increase in net prop-

erty after allowing for the increase or decrease in debts. It shows the sources of revenue and the amount obtained from each. It classifies all expenses so that it is possible to make comparisons with other firms in the same line between one period and another and between one department and another. These comparisons are made not only for totals but also for detailed items. Thus, railroad expenses are subdivided into 122 items, each one of which corresponds to some amount of performance. From these reports the operating offices can tell not only that expenses have increased a certain amount but just where their increases have occurred; perhaps, the increase was due to injuries, floods or to an increase in traffic or to any one of a number of other things. Even though expenses show no increase they may still be too high as shown by the costs of other roads operating in the same territory. From these accounts, may be discovered the cost per unit of work done, for instance, locomotive repairs per locomotive mile or per car mile or per tractive ton mile. The same is true of other classes of equipment and of ties, rails, fences, etc. The expense accounts number 122 but this is just the number reported to the Interstate Commerce Commission. The railroads for their own statistical purposes keep many more. Cities are now waking up to the statistical use of accounts. The city of Denver has the expenses incurred by its police department split up according to the following headings, each of which is further subdivided: administration, operation and maintenance of police telegraph system, policing the city, special police protection, regulation of traffic, detection of crime, operation and maintenance of police ambulance and patrol, detention of prisoners—adults, detention of prisoners—juvenile, and miscellaneous. The cost of other departments is similarly divided. Costs should not only be classified according to the purpose of function of the work done but also according to the kind of work. For instance, the expense of an automobile used by the chief of police would be charged to the police administration account which is charging on the basis of function but it should also be charged to an automobile account so that the city would know how much it is paying for the use of all automobiles. This account should be supported by a detailed record of each machine so that information would be at hand to eliminate inefficiency in their maintenance and to serve as a guide to future purchase. The following is a page of such a record:

Department —.

Feature —. Operation of Automobile.

Remarks —. E. M. F. —. Cost \$1,300.

Mileage this month, 1,175; total to date, 8,066.

Account Number.	Classification.	This Month.		Total to Date.	
		Amount.	Unit Cost.	Amount.	Unit Cost.
	Supplies:				
1	Gasoline.....	\$25 10	\$.023	\$215 67	\$.0249
2	Lubr. Oil and grease.....	7 49	.006	73 59	.0093
3	Other supplies.....	2 70	.002	95 64	.0093
4	Storage.....	5 00	.004	40 50	.005
5	Tire repairs.....	115 53	.097	354 77	.044
6	Other repairs.....	47 90	.042	298 29	.038
7	Depreciation.....	26 07	.022	411 46	.052
8	Miscellaneous.....	1 00	.001	7 33	.0009
	Driver's salary.....	100 00	.085	1,027 40	.1271
	Driver's expenses.....	8 80	.007		
	Total.....	\$339 59	\$.289	\$2,524 65	\$.313

The following statement of receipts and disbursements of a municipality owned water works together with the accompanying revenue and expense statement shows how much work has to be done before one can tell the amount of the revenues, of the expenses and of the profits and the present disposition of those profits when only receipts and disbursements are given:

WATER DEPARTMENT.

Receipts.

Water rates	\$106,352 62
City's payment for public use of water..	17,549 10
Plumbers' licenses	150 00
Loan at Bank	2,500 00
Miscellaneous	335 03
	<hr/> \$126,886 75

Disbursements.

Bonds paid	\$25,700 00
Interest on bonds	18,049 00
Salaries	17,371 90
Repairs to mains	460 21
Repairs to hydrants	1,082 61

Tools and utensils—replacements	\$495 33	
Supplies and Repairs to stations	5,583 32	
Fuel	12,319 77	
Barn expense	1,987 94	
Repairs to service		
Office expense	1,131 27	
Miscellaneous Repairs	974 94	
Insurance	190 77	
Miscellaneous expenses	2,156 23	
Reconstruction	4,332 08	
Pipe extensions	23,259 79	
Improvements to stations	7,650 03	
		\$124,320 75

The difference between the receipts and disbursements is \$2,566, that much more cash has been received than paid out. Has the profit, therefore, been \$2,566? The fourth item shows that \$2,500 was gotten by borrowing and you can not include that in your profits. Money cannot be made simply by borrowing it. The other items are probably revenues—that is, value that had accrued to the department from the sale of its services for the period. They are not, however, the entire value of the services rendered for some of the water delivered during the year has not yet been paid for. The department has a good claim against these people who have not yet paid. It is an amount which was earned in this period but which will not be paid until the future. Of course, if the city wanted to, it could make all delinquent customers pay promptly by turning off the water but they will pay in a little while so why resort to such measures. The point is that not all the revenue earned in this period is in the form of cash; some of it is in the form of accounts receivable. The cash receipts, here, probably contain some collections of revenue earned in past periods and it is assumed that the revenue earned in this period but still in the shape of claims and therefore left out equals the items put in but not earned during this period. Assumptions are always dangerous and a good account system makes as few as possible. Here there is no excuse for making one. In fact, a good accounting system would get the amount of revenue outstanding as a by-product in checking up bills outstanding.

The next item about which there may be question is the city's payment for the use of water. This may equal the value of the

service rendered or it may not. In this case the value of the water furnished the city exceeded the payment received from the city by \$7,950.90, which however is not obtainable from the statement as furnished but was established by independent investigation. When a city operates a utility, that utility should be individualized. The stockholders of a corporation are not the corporation and the city is not the water department. The city's relation is that of owner and manager. It is not necessary that the city actually pay over the cash to the water department only to receive it back later in the form of profits but it is necessary that the water department be given credit on its books for the value of all services furnished by it. If water furnished to the city is not charged for at its correct value, we make two errors—first, that the expenses of the water department appear a much larger percentage of the revenue than they really are, and second, that the expenses of running other departments of the city appear much smaller than they are. The grocer who takes home groceries ought not to regard them as an expense or cost of his sales but as a withdrawal of his profits. So here, water taken by the city and not paid for is an additional revenue, the money for which never actually changes hands. The total revenue under the assumption made consists of water rates, total value of water furnished the city, plumbers' licenses and miscellaneous totaling \$132,337.65.

Are the cash payment equal to the cost of furnishing the water? The first item is Bonds Paid, \$25,700. This is not a cost of this period. True you have that much less cash but you have also freed your property from debt so you are no poorer. No one ever grew poor by paying his debts. If the people have paid all their debts of \$550,000, the first year the plant was in operation that would not have made the cost of furnishing the water that year \$550,000 more than it otherwise would have been for although they have parted with that much cash they now own their plant. It is simply a purchase or exchange in which you give up cash to obtain a greater equity in the business. The cost of operating is not increased thereby. Interest on bonds is evidently a different kind of item than salaries, fuel, etc. These last are operating charges and the man who is responsible for their size is the operating official, but interest on bonds is a financial charge and the amount of it is dependent not upon the operating officials but upon the decision of the citizens themselves; they have decided to borrow the money to buy the plant instead of contributing it themselves. We will leave it out for the moment. Extensions and improve-

ments are not expenses. They are like bonds paid above. The cash paid for them has been converted into goods or benefits which we have at the end of the year. If you have a thing at the end, it can not be a cost, for costs are sacrifices and here you have sacrificed nothing. You have merely converted it. The rest of the items are expenses and total to \$49,661.93 making a net operating profit of \$82,675.72. To get the profit belonging to the city, we must next subtract the Interest on Bonds or \$18,049, which leaves a net income of \$64,626.72. It is impossible to tell whether these are all the expenses or more than the expenses for we have only cash paid to go by. Some of the fuel used this year may have been paid for the preceding year and so have been left out of our calculations. On the other hand, some of the fuel bought this year may not be used till next. It is impossible to tell, so we will assume that the expenses omitted equal approximately the items included which are not expenses.

The Revenue and Expense Statement is as follows:

Revenues.

Water rates	\$106,352 62
Value of water furnished the city	25,500 00
Plumbers' licenses	150 00
Miscellaneous	335 03
<hr/>	
Total revenue	\$132,337 65

Operating Expenses.

Salaries	\$17,371 90
Repairs to mains	460 21
Repairs to hydrants	1,082 61
Tools and utensils—replacements.....	495 33
Supplies and repairs to stations	5,583 32
Fuel	12,319 77
Barn expense	1,987 94
Repairs to service	1,575 56
Office expense	1,131 27
Miscellaneous repairs	974 94
Insurance	190 77
Miscellaneous expense	2,156 23
Reconstruction	4,332 08
<hr/>	

Total operating expenses \$49,661 93

Net operating revenue.....	\$82,675 72
Interest on bonds	18,049 00
<hr/>	
Net income or profit	\$64,626 72

Note:—No allowance has been made for depreciation.

The profits having been determined, the next question is where are they. The profit together with the \$2,500, which was borrowed, making a total of \$67,126.72, have been disposed of as follows:

Given to the city in the shape of free water	\$7,950 90
Retained in cash	2,566 00
Bonds paid—purchase of a greater equity in the business	25,700 00
Extensions	23,259 79
Improvements	7,650 03
<hr/>	
Total	\$67,126 72

In order to get information of real value, the statement as furnished has to be completely made over and the result of such recasting is a statement containing many approximations and owing to the lack of proper classification, it is often impossible to get as much information as we have here obtained.

It would seem to the layman that to get out all these statements and details would involve considerable labor and cost. Even if it did, the cost would be amply repaid by the results attained as is shown by the fact that precisely, where competition is keenest, are to be found the best accounting systems. Much information comes as a by-product. You have to know the total tax levy at the beginning of the year for only by so doing can you fix the tax rate. You must know the amount collected by the treasurer in order to know for how much cash he is responsible. It is little trouble then to find out the total taxes outstanding. You almost have to get this figure to be sure that you have charged the treasurer correctly for by adding the paid and unpaid taxes together and comparing them with the total at the beginning, you get an absolute check on the arithmetical accuracy of your work. The same is true of other items. Wherever you must keep a great deal of detail, you need one account for mains and accounts.

University of Michigan, Ann Arbor.

A CONTRIBUTION TO THE THEORY OF TAX-SHIFTING.

R. S. TUCKER.

One of the points in the theory of incidence of taxation on which a large majority of economists are agreed, is the doctrine that taxes on real estates are divisible into two parts—the tax on the land and the tax on the building, and that the first of these cannot be shifted away from the land-owner but the second results in an increased rent to the tenant and is thus shifted to the consumer of building utilities. This theory is stated by Smith, Ricardo, Mill, and more recently by Professor Taylor. I quote: "It is almost certain that, of the total tax collected from the owner of a house and lot, one portion is really paid by him, while another portion is in the end taken from the tenant in the shape of higher rent; and, what is more significant, for our purpose, it is also quite certain that the dividing line between these two parts corresponds pretty closely to the line which separates that portion of the total value of the place which constitutes the value of the lot, from that other portion which constitutes the value of the house."^{*}

Bastable qualifies the simple theory by declaring first, that a tax on ground used for building may to a very slight degree be shifted by the withdrawal of certain sites nearly as well adapted for agriculture, and secondly, that an attempt to increase rent in order to pay a tax based on building value will check the demand for houses, thereby throwing some of the tax on the owners of existing houses and some of it on owners of vacant sites for which the demand is lessened.

What I desire to show in this paper is that the division of the tax on real estate into two parts is only formal and without much real significance; that in the case of a tax based on capital value, or selling price, the forces which bring about shifting are the same in nature whether the tax be levied on the land alone, or on the combined value of the land and the building. I think we will all agree that a tax on the sole use of a commodity will have as injurious an effect on the demand for that commodity as a tax on the commodity itself would have. If for example shoe-polish were a fixed supply good, a license fee charged on boot-blacks, a duty on the act of having your shoes shined, an excise on polishing

^{*}F. M. Taylor, *Readings in Economics*, P. 182.

brushes, and even perhaps a head tax on Greek immigrants would all act to cut down the demand and hence the price of shoe-polish. The only limit to this decline in price (assuming as we do that the cost of production need not be considered) would be the alternative use of shoe-polish in blacking stoves and the demand price for it for that purpose. But not all kinds of polish can be used on stoves.

In the same way a tax on the use of urban land for buildings, whether it be a tax on the building, or on occupier's rent or on the citizens or industries of a town, or on the land itself, must reduce the demand for land for building purposes in that town. This is particularly the case with a local tax in a locality exposed to the competition of neighboring taxing districts equally or nearly as well adapted for the residential or industrial needs of the population. The effect of any such tax will be to reduce the demand for land for building purposes, either because the demand of tenants has fallen off or because the costs of supplying buildings have increased. The land itself is very nearly a fixed supply good; its price is determined by demand and is limited by the profit obtainable by building on it, i. e., the difference between the rental that tenants will pay and the necessary costs of maintenance and repair, including taxes. This difference capitalized at from 4 to 10%, according to local circumstances, is the price of the land. (Occasional sales showing rates of capitalization on net yield higher or lower than this are usually based not on immediate yield but on speculative values.)

It is obvious then that anything which tends either to lessen the demand for buildings or to increase their cost must result in lower land values in the locality affected. This is true not only of taxes but of industrial influences.

It is of course not a complete answer to the problem of proper distribution of taxes to say that the incidence is here or there; the effect of governmental expenditures must also be taken into account. Moreover we can not neglect the presence of economic friction and the consequent necessity of allowing a sufficiently long time for existing leases to expire and for tenants to adjust themselves to changes in conditions. All I wish to take up in this paper, however, is the underlying law of shifting.

What is it that determines the demand for buildings in any given community? In the case of business buildings it is the opportunity to make money by locating there, and this in turn depends largely on the number and buying power of the residents. In the

case of dwellings it depends partly on the amenities of life, the attractiveness of the town as a place of residence, and partly on the opportunities for profitable employment. There seems to be a close relation between wages and rentals, if we compare one year with another in the same place, and also if we compare different places at the same time. Statistical investigations show a very small variation in the ratio of rent to family income, for incomes of the same size and families in the same locality. In fact it seems reasonable not only to regard the rent of a site as a residuum after deducting the necessary expenses connected with utilizing the site from the rental obtainable, but also to regard the rental paid by an individual for this housing accommodation as a residuum obtained by deducting from his total income the necessary costs of living, such as those of food, clothing, and fuel. It has been said, for example, that one reason why house rents are lower in Boston than in New York is because the price of food is higher. It is a well known fact that neighboring suburbs are continually competing for prospective residents, and that in the district which has the best accommodations, especially schools, the rentals of identical buildings will be higher than in the rival districts.

I said that land is practically a fixed supply good. The proportion of land which might be added to the natural supply of sites by means of extraordinary outlays is very small—so small that we may fairly declare that the supply is incapable of enlargement. On the other hand it cannot be greatly restricted. Land may be deliberately kept out of use, but this involves a great loss of interest and can only be done by wealthy owners, and only when land is not heavily taxed. In some cases land can be devoted to use which is not so highly taxed, e. g., agriculture, under the English system of local rates. But it is obvious that, if the profits to be derived from building are great enough to more than offset the added tax, the land owner, if guided by economic motives, will prefer to pay the tax for the sake of the extra profits. And if the system of taxation is one that minimizes the difference between the amounts paid in the two cases (i. e. if taxes are based on the selling value of property, or, even more, on bare land value) this preference will become almost a compulsion. The only exception will be when the owner anticipates a future increment in land value which is incompatible with immediate development and which is great enough to offset the loss of interest. Such an increment is rather uncommon, both because of the difficulty of anticipating the exact direction of suburban growth and because

compound interest mounts up so rapidly. Assuming 5% as the net return on land, the value of a site must double in fifteen years to make it profitable to hold it idle.

Although the effect of almost any kind of local tax is to reduce the value of land, and that of all well-planned governmental expenditures is to increase land values, it is not by any means a matter of indifference on whom and on what basis the taxes are imposed. Total value, land value, gross rental and net rental, though equally available for the tax-collector, do not stand in the same proportion to each other in a comparison of different properties. I mention this point only to avoid misunderstanding. Even if the owners as a class must in any case ultimately bear the whole incidence of taxation, the share of each owner would vary according to the base chosen, and the duration and incidental results of the process of shifting might be widely different; and I do not maintain that the *whole* incidence of local taxes is on the land-owners.

It is a matter of common knowledge that not all pieces of land are fit for building sites, and that the difference in value between those that are and those that are not is not determined by the expenditure on the land, in laying out streets, putting down sewers, and so on, plus the original value of the land, if any, for agricultural purposes, but depends on the demand for building accommodation in that particular locality, and the cost of constructing the kind of accommodation demanded. It is not so commonly understood that there are among the higher grades of land relations similar to those between suburban agricultural lands and building sites. If for example a certain site is well suited for a bank or a department store, it will not for long be devoted to any other form of development, for such sites are rare, and the return to the land will be much greater, over and above the costs of build-and maintenance, than if a warehouse or a tenement were put on the site. Occasionally the difference in site rent to be obtained from two competing methods of exploitation is slight, but in most cases the difference is very great. It may not always be certain that the development which promises the most site rent is bound to succeed, but granting its success it will usually yield much more than any other development could.

Marginal land for any kind of development is land on which capital invested in that certain way would yield, besides a reasonable return on the capital, no more than would be earned by the land if developed in some other way. A tax on buildings on such

marginal land would obviously be placed by users of those buildings, and if they refuse to pay, the land will be devoted to some other use. But land that is marginal for some specific use is not necessarily no-rent land, or even land without a site-rent. Before a site becomes even worthy of consideration for the purpose of erecting a bank or an office building it must have a pretty high site value for other purposes. The more valuable the site for the purpose for which it is used, the less will taxation affect the building, and in cases where the site is much more valuable for that purpose than for any other it may be that all the taxes on the property fall on the site and the building may go scot-free. It may be, for example, that a piece of land is well situated for a moving-picture theater, and will earn a much better rent for this than for any other purpose. Its selling price will be somewhere between its value for some other use and the value obtainable by capitalizing all the profits of the theatre after deducting necessary expenses, including taxes. Which extreme of this range becomes the actual selling price will depend on whether the demand of would-be theatre owners is greater or less than the supply of available sites.

Now it would be easy to say, off-hand, that the incidence of a tax on moving picture theatres would be on the theatre-owner or on the public, if the demand is greater than the supply of suitable sites, and on the land-owners in the opposite case. This conclusion, apparently so simple and certain, is absolutely contrary to the facts. If the demand exceeds the supply the actual price will be fixed by the marginal demand price and the first extra-marginal demand price. A tax will cut down both of these and thus reduce the price, so in this case the tax falls on the site.

On the other hand if the supply of suitable sites exceeds the demand, the selling price is fixed by the marginal and first extra-marginal sellers' prices and there is nothing in the tax to make them change their estimates and accept less than if there were no tax. Hence the tax must be borne by the theatre-managers or the theatre going public.

Incidentally it may be remarked that this same line of argument applies to the incidence of increment taxes. One of the commonest statements as to the incidence of these is that when the demand for the land is great the incidence will be on the purchaser; when the demand is not so great the tax will fall on the seller. But if the demand is great, that is what determines the price, and a tax on increment, collected as it is from the seller, cannot increase the

price; while if the demand is small, supply price is what sets the price and that may be increased by an increment tax.

What is true of moving pictures is true, *mutatis mutandis*, of a general tax on buildings. If a site is much more valuable for an expensive form of exploitation than for a cheap one, it will be used for that form and taxes on it will be borne by the site owner until the whole differential advantage is eaten up. If all urban and suburban land could compete for all kinds of uses, then a tax on any method of exploitation would have to be borne by those who desired to exploit land in that way. But in real life we find not a continuous series of sites each a little less valuable than the last, but distinct series for each particular kind of development, with great breaks both within and between the series. The incidence of a tax, say on skyscrapers, is absolutely unaffected by the potential competition of sites five miles from the business district, or by the possible use of business district sites for agricultural purposes.

We must abandon the Ricardian idea of rent when discussing urban values. Except to some extent for residential purposes, the value of land is not dependent on its superiority over another site, but on its actual value for the use to which it can best be put, whether or not there is another site adapted to the same method of utilization. We must restore Smith's definition of rent—the excess of income over necessary expenditure and reasonable profits—to the throne from which it was expelled by the differential idea. In this belief I am supported by the theory and practice of all real estate men with whom I have discussed the matter.

There is especially a very noticeable break between agricultural land and building land, due partly to the nature of the outlays necessary to prepare land for building, the risk of the enterprise, and the long time needed before profits can be realized even when the adventure is successful. The growth of cities is not steady in all directions but fitful and in unanticipated directions. Land agents who are lucky make immense profits, others incur immense losses. A new car-line will suddenly increase values in the district served, but it may incidentally ruin land development schemes in some other district. For this reason the contention that the value of land for agricultural purposes constitutes a foundation on which land-owners can plant themselves in resisting attempts on the part of builders to shift building taxes on to them is erroneous. The foundation is there, but it is so far below the actual price levels and so detached from them that in many cases it is

of no more assistance to land owners in the struggle to avoid tax burdens than the bottom of the ocean to a man struggling in the middle of the Atlantic.

Having discussed the case of a site adapted for different uses, let us take up the case of several sites competing with one another for the same use, all of them being above the margin for that particular use. The simplest case is that of residence land.

The effect of higher costs of buildings in checking demand we need not consider at length. The demand for housing accommodation among most social classes seems to be fairly elastic, and to the extent that it is, taxes obviously cannot be shifted on to tenants in the shape of higher rents, for they will put up with less accommodation rather than pay more. When this occurs the tax, whether on building or land, will probably fall to some extent on all landlords, but all except the owners of the most expensive residence sites will be able to replace a large part of the tenants they lose by other tenants formerly dwelling in more expensive apartments, and thus escape a large part of the burden. The most expensive sites however have no such relief.

But even when the demand for housing accommodation is not at all reduced by an increase in rentals or a tax, I shall attempt to show that the traditional distribution of the incidence between building and site is unwarranted.

This reasoning covers the two classes of persons whose demand for housing is according to Professor Seligman *inelastic*—those who are too cramped already to be able to get along with less than they have and those who are so wealthy they are unwilling to get along with less. It can best be brought out by studying a few typical cases. Suppose a man with an income of \$2,500 a year choosing between a central and a suburban dwelling. There are three possible hypotheses; (1) he has no preference and is guided only by pecuniary motives; (2) he prefers to live in the city; and (3) he prefers to live in the country. In the first case he will estimate the extra amount he is willing to pay for the central site by considering the saving in car-fare and in time, which we will put at \$5 a month. We will assume that the type of house he desires could be supplied at a rent of \$25 if there were no taxes and no ground rent. The city lot obviously has a site rent \$5 greater than the suburban lot, and it will not invalidate the argument if we take the ground rents to be respectively \$5 and nothing.

Now suppose a tax on gross rental, collected from the tenant, of 25%. Since we are assuming that the tenants demand is inelas-

tic, the tax will be added to the rent. The suburban house will cost \$31.25, and the urban one \$37.50. But the difference which the tenants is willing to pay is only \$5.00. The extra \$1.25 must come out of the site rent; it equals 25% of the site rent in this case, which has induced Pierson and others to lay it down as a rule that the tax will be divided proportionately between the building and the site.

But if we take the second case, and assume that the man would really prefer to dwell in the city the result is somewhat different. This preference will show itself by his paying somewhat more, or taking a somewhat poorer house, or both. Which, and to what extent, is hard to determine. Suppose we assume that he will spend \$35 for a house in the city, untaxed, the house itself being worth \$20, which, of course, leaves \$15 for the site. The suburban house is the same as before, \$25. A tax of 25% on gross rental would naturally raise that of the city house to \$42.75, and the other to \$31.25, a difference of \$12.50. But the city house is only \$10 more desirable to the tenant, so the \$2.50 must fall on the site. It is not however 25% of the *site value*, but only 25% of the *difference in rent between the two competing houses, including both their site and building values*.

The opposite case may now be taken, the man who naturally prefers to live in the suburbs. He will not live in the city unless he can get as good a house at a price which will make his total expenses less, or else a better house for the same outlay. He will pay \$25 in the country, \$28 in the city for a similar house, or \$30 for a house worth, as a house, \$27 on a site worth \$3. Add the tax at the rate of 25% and the houses will cost, respectively \$31.25, \$35, and \$37.50. The tenant's estimate of the advantage of city life is only \$3. Therefore he will pay only \$34.25 for the smaller city house, or \$36.25 for the larger. The difference (\$0.75 or \$1.25) must come out of site rent, but it is not necessarily proportioned to site rent. It is always a proportionate part of the estimated differential advantage of one competing house over the other, and this may be equal to site rent, or greater, or less.

So far I have discussed a tax on rental collected from the tenant. Except for the initial difficulty in shifting while existing leases are in effect, the ultimate result of a property tax ought to be nearly the same, if we assume that the tax can be shifted at all, i. e., if we assume an inelastic demand.

As the value of property is the capitalization of net income, the property with more valuable sites will be taxed more under our

American system than under the gross rental tax, for site rent is nearly all net rent whereas building rent contains a large element of repairs, expenses of management, etc., which must be deducted before capitalizing. Moreover site rent is usually capitalized at a lower rate of interest. So under a property tax there is a tendency for a larger proportion of the tax to fall on the site than under a tax on rental.

There is a kind of incidence of taxation, if incidence be the proper word, which results in certain tenants getting less accommodation than they would if there had been no tax, and certain site-owners being unable to earn any profit or site rent because of the decreased demand of tenants. But in this case there is no tax paid. If property becomes less valuable as a result of a property tax, or if rentals decline as a result of a tax on them, then the amount of tax paid is less; and where there is no tax it is incorrect to speak of incidence. This is not the case contemplated in the present discussion.

To summarize: (1) Any kind of a tax on the most profitable mode of utilizing a site tends to reduce the value of the site to that point where, under the circumstances, it becomes more profitable to develop the site in some other way. (2) A tax on real property is not necessarily divisible into a tax on the house and one on the site in proportion to their respective values, but its incidence depends on the willingness of the tenants as a class to restrict their accommodations, or to change their nature, and on the possibility of doing so. As a matter of observation it would seem that, in the case of American cities with many computing suburbs, the proportion of the tax on real property that falls on the site value is usually greater than the proportion of site value to the total value of real estate taxed.

From this discussion it would appear that any attempt to draw up rules for the proper apportionment of taxes so that after the process of shifting is completed the taxes will be borne by those whom it is desired to tax, must fail because of the complexity of the problem. But one practical consideration makes the outlook less discouraging. That is, that generally the benefits of local expenditures will be transferred at about the same rate of speed as the burdens of taxation, and if taxes are levied in the first place on the persons who are directly benefited by their expenditure they will probably fall in the end on the persons who receive the ultimate permanent benefit. This would mean adopting the one good feature of English local rates—assessment on the occupier.

The effect of this system in increasing the number of voters directly interested in the economical management of local affairs I cannot discuss at the present time. This is a paper on theory, and I think I have already proved what I set out to—that no clear-cut line can be drawn between the incidence of taxes on sites and taxes on buildings.

University of Michigan, Ann Arbor.

BOTANY.

PATHOPHYTES AND PHARMACOPHYTOLOGY.

A. D. BUSH.

Limiting the present discussion to what affects directly the human body it may be stated that the vast majority of disease-producing plants belong to the group of Schizophyta or fission plants, of which the Bacteria are the most important. The Bacteria may be classified morphologically as Micrococci, Bacilli and Spirillae, each of which has distinguishing characteristics and properties. The normal growth of these plants in such a favoring habitat as is afforded by the warmth and moisture of the human body, is accompanied by the generation of waste products of remarkable toxicity. If unneutralized, these products when absorbed by the invaded organism become highly inimical to the vitality of several tissues, especially those of the nervous centres. With some groups the metabolic activity rapidly produces necrosis of the adjacent animal cells, a process which, if taking place in the spinal cord (as in infantile paralysis, for instance) rapidly produces severe disturbances in correlated parts. In any case, but especially in nervous tissue, the plant in its growth activities produces by both mechanical and chemical means a violent inflammatory reaction, locally, as the system attempts to protect the part from deleterious foreign material. This reaction is accompanied by an exudate whose mechanical pressure is an additional factor in lowering vital resistance and in disturbing function.

Briefly reviewing the several groups we find that among the Micrococci the principal diplococcus is the one causing cerebro-spinal meningitis. Streptococci are bacteria producing erysipelas, puerperal fever, many nose and throat affections, middle ear disease, some of the more serious bone and joint troubles, and probably scarlatina and measles. The staphylococci are responsible for various boils and abscess formations of both skin and bone. The micrococcus lanceolatus produces lobar pneumonia and other serious infections of serous membranes. The gonococcus is the social scourge and, aside from the general misery for which it is the responsible factor, is productive of most of the blindness in the

world and of most of the troubles resulting in surgical operations on women.

The Bacilli constitute a large group, various members of which are the causative factors in wide-spread disorders. The bacilli of Diphtheria, Glanders and Influenza find their most favorable habitat in the nose and throat primarily, and secondarily in the nervous system; the bacillus of Whooping-cough, in the trachea; the bacillus of Tuberculosis, most frequently in the lungs though it may attack any structure of the body. The bacilli of Yellow Fever and Typhus Fever are primarily active in the alimentary tract and in the red blood corpuscles; the bacilli of Typhoid Fever, in the glandular structures of the small bowel; the bacillus of Bubonic Plague in the general lymphatic glands of the body; and the bacilli of Leprosi and of Anthrax in the dermis and sub-cuticular structures. Each of this group produces primary local reaction of variable severity followed sooner or later, if unchecked, by a profound systemic reaction.

The principal spirillae consist of the relatively mild one productive of Relapsing Fever; the virulent one causing the acutely exhausting Asiatic Cholera; and the one producing the persistent degeneration of circulatory and nervous systems known as Syphilis.

Besides the Schizomycetes some of the higher Fungi are instrumental in causing painful though less dangerous troubles, consisting chiefly of indurated inflammations of the skin and mucus membranes. Aphthous stomatitis, or thrush, is due to one of the saccharomycetes, *Oidium albicans*, Ringworms of the scalp and body are produced by several of the moulds, *Achorion* and *Trichophyton* especially. One of the *Streptothrix* is responsible for the form of tissue necrosis known as Madura foot.

Turning now to the consideration of pharmacophytology we may note the curious and interesting fact that the most powerful of medicines, the alkaloids, also represent waste products arising in the course of vegetable protein katabolism. As it is the toxin waste of the lower fungi that produces serious and dangerous reactions within the human body, so it is similar substances derived from the spermatophytes that are used as medicines for combating some of the symptoms arising from the activity of the lower organisms. In each case the disturbing substance within the body is a vegetable product poisonous to that body, but the substances used as medicines are kept under careful control so as to exert a toxic influence on the infective germ before such an effect is produced on the harboring body. Or in cases where such direct action is not

possible, the drug poison is used to stimulate the body to such a degree that in the resulting reaction the infective toxin will be incidentally neutralized. Usually, however, the effect of vegetable drugs is simply to so modify systemic processes as to prevent that excessive reaction of the body which of itself might readily prove inimical to the welfare of that body. The actual curative value of most of the alkaloids is either nil or very small; they simply serve as a more or less effectual aid to nature in time of need. For purposes of cure chief dependence must be placed on natural or artificial production of immune bodies or antitoxins.

It may be said, therefore, that the vegetable alkaloids do not directly antidote the poisons produced by the infective fungi. Their principal value rests in their power to produce a more or less complete antagonistic reaction of the several tissues of the body. For example, the exhaustive drainage from the intestines produced by the bacillus of Asiatic Cholera may be partially prevented by the counter action on the secretory and osmotic processes exerted by Morphine. Or again, the cerebral irritation produced during Typhoid may sometimes be offset by Opium, or the mental depression accompanying Typhus may be partially counteracted by Caffeine. This, of course is purely symptomatic treatment, reliance for cure being placed on the normal acquirement of immunity either by the body itself or through the medium of some other agent in which high protective immunity has been earlier induced.

Our principal alkaloids used in medicine are derived from the angiosperms. From the Ranunculaceae is obtained a mild gastro-intestinal stimulant Hydrastis, and from another member of the same family, *Aconitus napellus*, is obtained an important cerebro-spinal depressant. From the Solanaceae are derived an excellent antispasmodic, Atropine from *Atropa belladonna*, and a related cerebral sedative from *Hyoscyamus niger*. Caffeine, our leading heart stimulant, and a well-known cerebral excitement, belongs to the group Rubiaceae, to which group also belongs the related *Cinchona officinalis*,—a plant whose alkaloid is highly toxic to the plasmodium of malaria. Cocaine, of the group Sterculaceae, is a motor excitant of the brain and cord, but when locally applied, is an inhibitor of the nerve impulses of sensation.

Morphine, derived from one of the Papaveraceae, is our most reliable analgesic in non-neuralgic pains, a valuable antispasmodic, and a narcotic of the first class, though so interfering with functional activity as to render somewhat slow and difficult resumption of normal activity. Physostigmine, of the Leguminaceae,

and Pilocarpine, of the Rubiaceae, are both depressors of the motor side of the spinal cord, an activity that may be effectively antagonized by Atropine (of the Solanaceae). Strychnine, of the group Loganiaceae, is a powerful excitant of the spinal cord, greatly heightening ease of sensory-motor response thereby facilitating reflexes of a spasmodic type.

From the group Apocyanaceae is derived a glucoside, Strophanthin which is an exceedingly powerful stimulant of heart muscle, being in fact a cardiac paralyzant in any but minute doses. Another important glucoside is Digitoxin, from *Digitalis purpurea* of the group Scrophylariaceae, which also powerfully affects the heart muscle rendering its diastole more prolonged and its systole more energetic and complete.

These are but a few, though perhaps the more important, of the vital relations existing between plants in the causation of disease and plants in the treatment of disease. An adequate consideration of these relations would fill many volumes, but this brief presentation may be of value in indicating one of the exceedingly important applications to life of botanical information.

Department of Botany, Olivet College, Olivet, Michigan.

A SIMPLIFICATION OF THE PRESENT FREEZING-POINT METHOD FOR THE DETERMINATION OF THE OSMOTIC PRESSURE OF PLANT SAP.

(Abstract.)

BY O. E. HARRINGTON AND R. P. HIBBARD.

The paper describes a simplification of the usual freezing-point method of determining osmotic pressure of plant sap. By this modification, instead of extracting the sap from the material and determining the freezing point of the extract, a determination is made directly upon the tissue which is in the form of a pulp.

The following are the essential features of the method: The material to be used is first carefully frozen, then ground in an ordinary food grinder, mixed, samples taken and placed in the freezing tubes and allowed to reach a temperature about one degree below its freezing point. Solidification is then brought about by turning the thermometer a few times to create a disturbance in the pulp.

Comparisons have been made between results, obtained in this way, with those obtained in the usual way upon the same material and it has been found that the closeness with which the results compare depends upon the thoroughness of the freezing and the thoroughness with which the sap is extracted. When a large press is used, with which it is possible to extract practically all of the sap, the results of the two methods check within the range of experimental error.

There are two special advantages of this modification. First, less time transpires from the time the preparation of the material begins to the end of the process, thus reducing the possibility of change in the composition of the material; second, a more accurate sample of the original material is used than is the case when the sap is extracted.

In as much as the results obtained by the two methods check within the range of experimental error when great care is exercised in the extraction of the sap, and in as much as the difference in results is greater when the sap is extracted less carefully, it is

believed that accurate results can be obtained more easily by this modified method than by the one in present use.

All of the work to date has been done, however, upon fleshy tissues and further work is necessary to show whether or not the method is applicable to drier tissues as well.

Michigan Agricultural College, East Lansing, Mich.

A SIMPLIFIED APPARATUS FOR MEASURING THE
CONDUCTIVITY OF ELECTROLYTES.

BY R. P. HIBBARD.

(Abstract.)

During the study of certain problems in plant physiology it became necessary to measure the concentration changes in culture solutions. The Wheatstone Bridge apparatus seemed fitted for this kind of work but it was later observed that there were many sources of error in the usual set up and the attempt was made to eliminate these as far as possible. As a result of our studies, we have not only simplified the method but increased its accuracy to a considerable extent. The modifications suggested also make the apparatus much easier to operate, thus eliminating to a great extent the "personal error." The correct bridge setting is made by the aid of the eye instead of the ear. The important changes suggested are as follows: (1) The induction coil is abandoned for a 60 cycle rotary converter on a current of constant potential. The Vreeland Oscillator is to be preferred to this but when this work was done the Vreeland Oscillator was not on the market. It has been shown that in assuming polarization at 60 cycles we are assuming something neither apparent nor real. We have used the frequency for a period of two years, and have had no trouble from polarization but what could be eliminated. (2) The Curtis Resistance Coils, wound for the annulment of capacity and inductance take the place of the ordinary resistances. (3) An alternating current galvanometer is put in the place of the telephone and in many ways is superior to the telephone tuned to any definite frequency. (4) The roller type of bridge with the "extended" wire should be used. The possible error from the use of the bridge thus modified would not be more than .002 of 1 per cent. (5) The construction, and the correct selection of suitable electrolytic cells for the different solutions necessitates more attention than is usually given. A preliminary report was published in the 15th Annual Report of the Michigan Academy of Science, 1913. The completed work has appeared as Technical Bulletin No. 23, of the Michigan Agricultural College Experiment Station.

Michigan Agricultural College Experiment Station, East Lansing, Michigan.

THE INFLUENCE OF AN INCOMPLETE CULTURE SOLUTION ON PHOTOSYNTHESIS.

(Abstract.)

BY O. M. GRUZIT AND R. P. HIBBARD.

We are far from possessing a precise knowledge of the rôle of the various mineral elements in plant life. They do not afford a source of energy like the organic compounds, carbohydrates, fats and proteids. There is much evidence to show that they are essential to the protoplasmic molecule and to regulate other chemical and physical conditions, which are at present so little understood.

We do know, however, that normal development is interfered with and in some cases inhibited when one or more elements are lacking in the culture solution. The studies reported in this paper were planned to determine, if possible what influence an incomplete culture solution exercises on the various, so-called vital activities of the plant, and more especially upon the photosynthetic process. The following table gives the amount of photosynthate made per ghm² in the different solutions.

TABLE I.

	Gain in dry weight per ghm ² .	Gain in dry weight per ghm ² .
Culture Solution.....	Exp. No. 1.	Exp. No. 2.
Complete.....	0.1557 gms.	0.1102 gms.
Distilled Water.....	0.2297 gms.	0.3236 gms.
Tap Water.....	0.2945 gms.	0.2468 gms.
Iron Omitted.....	0.2297 gms.	0.2361 gms.
Phosphorous Omitted.....	0.3380 gms.	0.3433 gms.
Nitrogen Omitted.....	0.1647 gms.	0.1592 gms.
Potassium Omitted.....	*0.0724 gms.	0.3650 gms.
Magnesium Omitted.....	0.2697 gms.	0.2585 gms.
Calcium Omitted.....	0.3128 gms.	0.4524 gms.
Sulphur Omitted.....	*0.0694 gms.	0.2457 gms.

*The plants had been injured and consequently these figures are not reliable.

These experiments were carried out in the green house during the month of February. Plants in the open in the summer time average twice as much photosynthate.

The following conclusion can be deduced from the above table:

1. The dry weight per unit area of leaves of seedlings grown

in the complete culture is less than that of leaves of seedlings grown in a solution lacking an element.

2. The assumption that the amount of photosynthate in leaves is an indication of energetic growth is far from true. In a complete solution as seen from the result, the leaves contain the least amount of photosynthate, while the solutions lacking potassium, calcium and phosphorus respectively, show the greatest gain in weight. This by no means indicates metabolic efficiency in plants growing in solutions lacking potassium, calcium, and phosphorous, respectively.

3. These results suggest that the explanation lies in a reduced translocation and a retarded photosynthesis. To test this, three sets of cucumber seedlings were grown in the various solutions. Two sets were used to determine the gain in dry weight per ghm². Before dawn the leaves from the third set were detached, the cut surfaces of the petiole sealed with melted paraffin and then returned to their respective solutions. The results are seen in Table II.

TABLE II.

Nutrient solution.....	Gain in dry weights.		Gain in % of detached over uncut.
	Uncut.	Detached.	
Complete.....	0.16974 gr.	0.65294 gr.	74%
Iron omitted.....	0.35160 gr.	0.65884 gr.	45%
Nitrogen omitted.....	0.29990 gr.	0.44760 gr.	32.9%
Potassium omitted.....	0.17850 gr.	0.25950 gr.	31.3%
Phosphorous omitted.....	0.64680 gr.	0.89920 gr.	28.1%
Magnesium omitted.....	0.10850 gr.	0.08920 gr.	-0.17%

It shows that the increase of dry weights of detached leaves exceed that of the uncut by a very large margin. It is also seen that the greatest per cent gain was in the complete solution, and that this is the average amount of photosynthate made under greenhouse conditions. This experiment further lends support to the hypothesis that the absence of an element retards translocation of the photosynthate. The above data also bear out the theory that the rate of photosynthesis is impaired when an essential element is lacking.

It must be remembered that this study is merely preliminary, but our present data in general indicates that the process of photosynthesis is greatly modified by absence of a certain element. The

modification apparently is expressed in the retardation of translocation and the reduced power in photosynthesis. Further work is in progress and a more detailed study of the various factors involved is being made and when this is completed the data will be printed elsewhere.

Michigan Agricultural College, East Lansing, Michigan.

THE HORMONE THEORY OF CHROMOSOME ACTION.

BY ERNST A. BESSEY.

That the phenomena of heredity are bound up intimately with those nuclear structures called chromosomes is the conclusion of almost all students of the subject. The reasons for this belief may be briefly reviewed. In ordinary nuclear division (mitosis), we find at one stage a continuous or interrupted thread (the spirem) becoming segmented into a definite number of pieces, the chromosomes. In plants all the chromosomes in a given nucleus are usually very similar to one another, but in many animals, e. g., some insects, they differ markedly. In the further course of mitosis, these chromosomes split longitudinally and the resulting halves are drawn to the opposite poles of the nucleus where each regenerates its missing half and they finally assume their places in the daughter nuclei. At the next nuclear division the same number of chromosomes appear and they will be found to have the same shapes and location as in the previous division. In fact this phenomenon is so widespread that biologists are now very strongly inclined to believe in the continued individuality of the chromosomes from one nuclear generation to the next.

Still more marked is the peculiarity of the behavior of the chromosomes in reproduction. Both the male and the female sex cells (gametes) are found to have the same number of chromosomes,* and on careful comparison these are found to match in the two cells. The zygote nucleus produced by the union of the two gamete nuclei has, then, a double set of chromosomes; i. e., two of every kind present in either of the gametes. Before the next sex cells are produced, there occurs that peculiar process called the reduction division or meiosis, in which the number of chromosomes is reduced again to the number found in the previous gametes. Careful investigation has shown that in this process one of each pair of chromosomes (which one appears to be a matter of chance) passes entire to one daughter nucleus while the other chromosome of the same pair goes to the other daughter nucleus. This process differs from ordinary mitosis among other things in that whole chromosomes not merely halves of the same chromo-

*I have left out of consideration here the sex determining chromosomes.

some pass to the opposite poles. The result is that every new gamete has *one* of each kind of chromosome present while the zygote nucleus and its descendants possess two of each kind.

The complexity of the process for exactly halving the chromosomes in ordinary mitosis and for properly distributing the whole chromosomes in reduction division makes it seem certain that the chromosomes play a very important role in the cell. The fact that the mode of distribution of the chromosomes at meiosis takes place exactly in the manner that the Mendelian theory requires for the distribution of the structures responsible for the main "mendelizing" characters has led further to the assumption that it is the hereditary characters that are borne by the chromosomes.

We talk very glibly about the "bearing of heredity characters." Just what is meant by this phrase? I feel it is a term that we all use very frequently without really considering what is included in the expression. We know, in general, that "like begets like." What does this mean in terms of cells and their activities?

Every plant and every animal develops from a single cell, the fertilized egg, leaving out of consideration the rather numerous host of lower plants in which sexual reproduction is lacking (Myxophyceae, Caulerpa, and scattered forms in other groups). The latter, although not producing eggs, mostly possess at one stage of the life cycle but a single cell. Even in those forms that are always multicellular we find that all parts of the individual arise by cell divisions or in case of coenocytes like Caulerpa by cell enlargement accompanied by nuclear divisions. Thus all the complex features of the structure of the most highly developed plants or animals must be bound up in the limits of the single cell which bridges the gap from one generation to the next. We may accept the theory of those who would greatly limit the complexity of these details by arguing, in many cases doubtless with right, that the development that any particular cell of a multicellular plant or animal undergoes is mainly merely a direct response to the immediate environmental conditions. But even then we must admit that there must be vast differences in the factors present within the nucleus of this cell to account for the fact that the eggs of different animals e. g., fishes, frogs, toads, not to mention the host of the aquatic invertebrates, and of many algae all develop into their own proper species although the external environment is identical.

The structure of the mature individual is a result of cell divisions and the modification of the resultant cells in various dissections.

There must be something inherent within the cells that determines just what each cell shall develop into in its own particular environment. In plants generally and to a large extent in the lower animals any group of cells is able to regenerate the whole individual, thus showing that the directive forces for all the structures of the individual are present in each cell and not distributed respectively among the various tissues. It is a fact that, in many plants as well as in most animals, the amount of cytoplasm that is carried into the egg with the sperm is very small or sometimes entirely lacking. Indeed, the important feature of fecundation appears to be the union of the male and female nuclei. This fact as well as the features of mitosis and meiosis to which attention has already been called makes it seem doubly certain that it is not only the nucleus but the chromosomes within the nucleus, that decide how the cells shall develop, and this means how the individual will be constructed.

If these chromosomes are of so great importance to the cell as the foregoing would indicate, how do they act? We must first of all consider their position within the nucleus. The "resting" nucleus as distinguished from the nucleus in the process of division may be described as a large vacuole of nuclear sap bounded by a tough plasma membrane of cytoplasmic origin, such as is always found where cytoplasm comes in contact with a body of water (e. g. at the exterior of the protoplast as well as the "tonoplast" around the large central vacuole). Suspended in the nuclear sap lies the tangled semi-fluid nuclear network consisting of a delicate thread on which are strung at various points irregular lumps of semi-fluid chromatin. A large drop of reserve protein (the nucleolus) chemically closely akin to chromatin is also suspended in the nuclear sap, apparently in more or less intimate proximity to the nuclear network. The latter may criss-cross through the central portion of the nucleus or perhaps more often lie near its circumference.

A closer examination of the relation of the chromatin lumps in the resting nucleus to the chromosomes that appear during mitosis makes it almost certain that the fine thread with the scattered chromatin masses on it is to be looked upon merely as made up of chromosomes stretched out and that these separated chromatin lumps are identical with the closely crowded deeply staining chromatin bodies visible in the chromosome. If now the chromosomes are the bearers of heredity it must be these scattered chromatin masses in the resting nucleus that have this function.

The question then is, how can these separate lumps of chromatin, each one perhaps the bearer of some separate trait, exert their influence upon the development and functions of the cell? The bulk of the nuclear network lies near the circumference of the nucleus, it is true, but not all. One can hardly conceive that only those chromatin masses do function that lie near the circumference. Even these it seems are not all in intimate contact with the cytoplasm but usually lie a short distance inward from the nuclear membrane.

To explain the action of the chromatin upon the cytoplasm various theories have been proposed. Perhaps the most popular of these is that of enzymes. We know that there are enzymes that will hydrolyze starches into sugars and others that change sugars into alcohol and carbon dioxide; some enzymes facilitate oxidation, others reduction; some digest proteins, others dissolve cellulose or the nearly allied pectose substances. These are however, all more or less catalytic in their nature; they facilitate certain chemical changes that would take place to a slight degree without their aid. It is rather hard to connect any known enzymes with the production of the peculiarities of morphology and physiology of the various cells of a plant or animal.

There is, however, another class of little known substances which exert profound effects upon the development of the higher animals. These are the "hormones," the secretions of some of the ductless glands of the body. As yet, much that has been written about them is in sore need of critical review, but yet enough is known to make certain of their existence and importance.

Probably the best known of these substances are the secretions of the thyroid gland, a ductless gland situated in the neck. If this becomes atrophied during childhood further development ceases, both physical and mental, and the child remains a dwarf, with the mind of a child, no matter how old he may grow to be. Let such a child be fed the extract of the thyroid gland of a calf, for instance, and development begins almost at once and normal growth and maturity, physical and mental, result, provided the thyroid treatment is continued. If it is finally discontinued various pathological developments of the skin ensue and finally a state of mind bordering on imbecility results. This can be cured, however, by resumption of the thyroid feeding. Another secretion of this nature is that of the pituitary gland situated at the base of the brain. In cases of hypertrophy of this organ there results the disease known as acromegaly. This is characterized by the elongation

of the bones of the extremities as well as by a thickening of some bones e. g., those of the skull. Other organs may also be enlarged abnormally. Most of the "giants" exhibited in circuses are persons afflicted with this hypertrophy of the pituitary body and the consequent acromegaly. The so-called secondary sexual characters of the males, such as the spurs, characteristic comb and coloring of the cock or the greater hairiness of parts of the body in other animals or even the characteristic shape of the body, are largely the result of such secretions into the blood stream from the male reproductive organs. By removal of these organs in the early stages of development in the individual these secondary characters are almost or sometimes entirely suppressed.

Other hormones might be cited but I believe I have made clear the far-reaching specific effects of these secretions, even when in small quantities. Some of these have been analyzed and have been found to be of not nearly so complex a composition as enzymes or proteins. They are, however, keys that fit the very complex locks, the protoplasm of the various cells of the body, setting free very important activities.

Now let us apply the foregoing to the chromatin masses that make up the chromosomes. Why can not we assume that the function of the different bits of chromatin that make up the chromosomes is to secrete substances similar to the hormones, nuclear hormones we might call them, which affect the cytoplasm and bring about characteristic reactions and activities in it just as the hormones secreted by the thyroid glands stimulate the continuance of the bodily and mental development, that from the pituitary body govern the growth of the bones, etc? Then the complete complement of chromosomes or, more correctly speaking, of the chromatin masses making up the chromosomes, secretes into the nuclear sap a mixture of many nuclear hormones which diffuse out into the cytoplasm. Here they stimulate activities and bring about a development of the cell to that structure and function typical for that particular organism.

In the case of hybrids we have coming into the cells different sets of chromatin masses from the different parents. In closely related parents some of the chromosomes or chromatin masses will be identical in their composition and secretions, but some will be different. In some cases these different secretions may not interfere with each other so that both paternal and maternal characters may show on a given structure. In other cases, however, one will entirely suppress the action of the other. Possibly the

fact that some crosses between nearly related plants never produce seeds may be due to the fact that the different nuclear hormones produced by the chromosomes of male and female origin within the zygote nucleus are so opposite in their effects on cytoplasm that the latter can not develop further and so no embryo is formed.

Department of Botany,
Michigan Agricultural College, East Lansing.

THE SEXUAL CYCLE IN PLANTS.*

BY ERNST A. BESSEY.

There are many groups of plants in which sexuality is entirely lacking. In some of these the indications are that this lack of sexuality is not due to its loss in the course of evolution from sexual ancestors, but that it is primitive; in other words has not yet been evolved. The Myxophyceae are good representatives of such plants. Possibly, also, some of the Protococcoideae which lack sexuality are to be classed as primitively sexless, but this is rather doubtful.

On the other hand we have numerous cases where the absence of sexuality is almost certainly due to its loss in the course of evolution from ancestors that possessed it. Thus we have in the Class Ascomyceteae a group of plants that, whatever theory as to their phylogeny may be accepted, have descended from forms possessing sexuality. This is borne out by the fact that a form of sexuality is present in most of the species of the class. However, the closely related genera *Eremascus* and *Endomyces* differ in this that the former possesses and the latter lacks sexuality. The same is true of the closely related family Saccharomycetaceae, the yeasts, in which ascus formation is preceded by conjugation in some forms and conjugation does not occur in others. Among the ferns, too, and the flowering plants there are quite a number of species in which the new generation is produced apogamously, i. e., without the sexual union. Perhaps the commonest example is the common dandelion (*Leontodon taraxacum* L.) in which the pollen still continues to be formed in spite of the fact that the embryo develops from an unfertilized egg cell. Such plants as these are therefore secondarily sexless.

What was the origin of sexual reproduction is not yet clear. Dr. Coulter is probably correct in his belief that the original gametes were modified zoospores. It is not so sure, however, that sexuality originated *de novo* at many different points in the Vegetable and Animal Kingdoms. It is indeed hard to conceive how the almost identical phenomena of sexuality in animals and the various groups of plants can have had separate origin. Indeed,

*Address of the retiring president March 29, 1916.

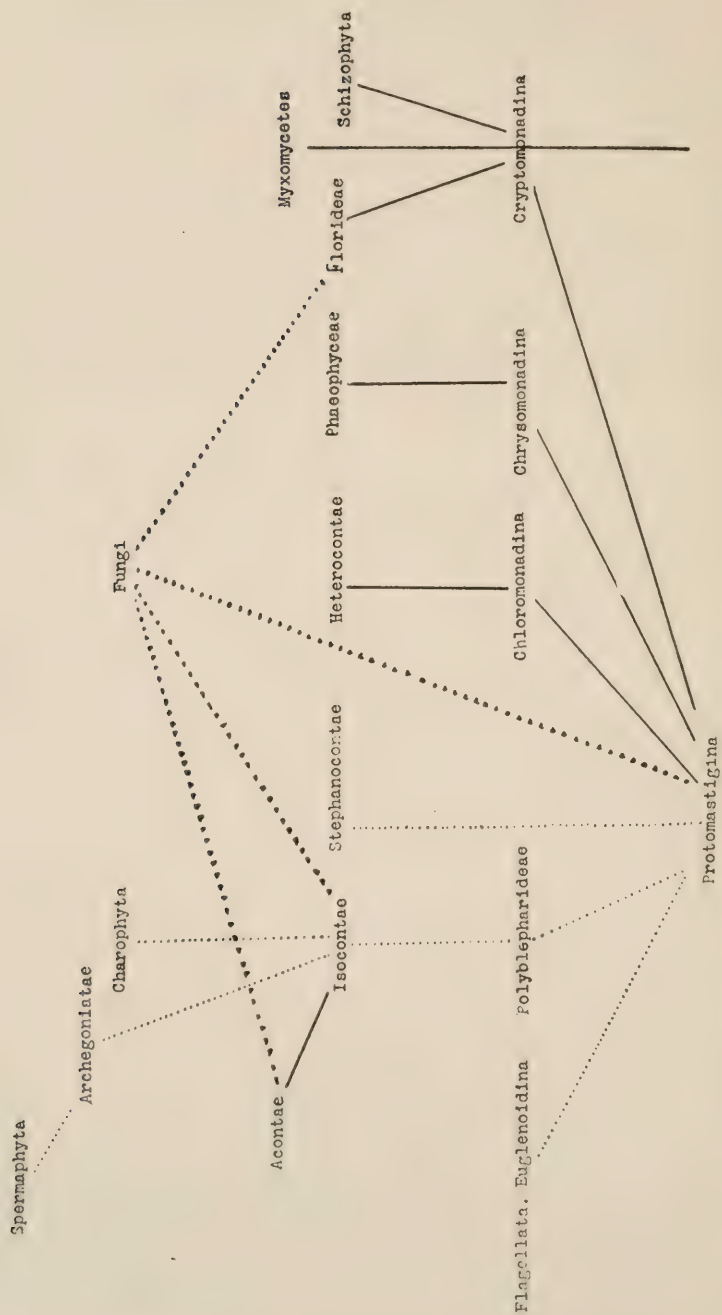


Figure 1. Lotz's diagrammatic scheme to illustrate his idea of the relationship of the various groups of plants.

the similarity of these phenomena is, if anything, a proof of the extreme age and common origin of this process in all organisms in which sexuality occurs.

I will digress here for a moment and suggest that any system of classification that disregards this ancient and common origin of sexuality will eventually have to give way to a system in which this is taken into consideration. I know that the currently accepted systems of classification as expressed by Engler and Prantl by Lotsy or by Oltmanns are in direct opposition to these views. The latter (and to a large extent the former) would derive all algae from those groups of Flagellata in which there is no sexual reproduction. These organisms are one-celled animals, some possessing and some lacking chlorophyll, motile by means of two flagella, and reproducing only by fission in the longitudinal direction. There are several groups which differ in the relative size of the two flagella, in the color of the chloroplast, in the chemical nature of the photosynthate, etc. Each of these is made by Oltmanns and Lotsy the point of origin of a different algal series. Thus the Heterocontae, the Peridineae and Acontae, the Phaeophyceae, and the Volvocineae-Protococcales-Chaetophorales complex all arise according to Lotsy from different, sexless Flagellate groups. (Figure 1.) Within each of these series sexuality is assumed to have arisen independently of the other groups. In so far as the higher animals, the Metazoa, are derived possibly from other groups of Flagellata the sexual process in these has still a different origin. This seems to me to be all wrong and I predict that the ideal phylogenetic classification of plants and animals will change this entirely and indicate by its arrangement of the groups of plants and animals the common origin of the sexual process.

What then are the essential features of sexual reproduction? The most obvious phenomenon is the union of two cells to form one (Fig. 2). In the most primitive organisms in which sexuality is known (and by primitive we mean organisms that have appar-



Figure 2. Union of similar gametes of *Hydrodictyon*. (after Coulter)

ently progressed least from the hypothetical ancestral forms) these uniting cells (gametes) are alike so far as the most careful scrutiny will reveal. However, as we follow up the various evolutionary lines we find that in most of these isogamy is prevalent at the base of the line with a gradual transformation to heterogamy toward the apex of each line. It is probably beyond dispute that this change from isogamy to heterogamy has taken place independently in many distinct lines. Thus in the Volvocales some species of *Chlamydomonas* are isogamous, but *Volvox* is heterogamous; in the Phacophyceae some species of *Ectocarpus* are isogamous and other species of the same genus show stages of heterogamy varying from merely a distinction of sluggish and actively moving, but otherwise indistinguishable gametes to an actual difference in size as well as activity. Higher up in the same great group we find that the larger gamete has lost its motility entirely. A similar development is seen in the Chlorophyceae as we pass from isogamous forms like *Ulothrix* or *Stigeoclonium* through various stages of heterogamy to forms like *Oedogonium* and *Coleochaete*. Even in the Conjugatae we find that *Mougeotia* is strictly isogamous while in the closely related *Spirogyra* there is a distinction of sex in that the protoplasm passes out of one cell (male) into another cell (female). Some of the Protozoa are isogamous and closely related forms heterogamous. However, in the Animal Kingdom heterogamy entered at a relatively earlier stage of evolution than among plants.

Let us return to the question as to what are the processes taking place in sexual reproduction. In plants like *Ulothrix* or *Ectocarpus* we see the union of two naked, motile cells of equal size. (Fig. 2.) In *Fucus* we see the union of small, motile almost colorless cells (sperms) with large non-motile, deeply colored cells (eggs). In *Spirogyra* the protoplasm of one cell crowds through a narrow conjugation tube to unite with the protoplasm of the other cell. In all these cases it is whole cells that unite. If we turn to the fungi we find in *Albugo* one or many (depending upon the species) male nuclei and probably some cytoplasm passing through a conjugation tube into the oogone; in *Pyronema* it is many nuclei and probably some cytoplasm that pass from the antherid into the trichogyne and thence into the oogone. In neither case, however, does all the cytoplasm of the antherid pass over, so that it is apparent that a union of complete cells is not necessary to the process. In the flowering plants the male cells enter the pollen tube as true cells, i. e., nucleus and cytoplasm, but in their passage down through

the tube the nuclei slip out of the cytoplasm so that it is only as naked nuclei that they enter the embryo-sac, and fertilization is accomplished by the entry of one of these naked nuclei into the egg.

It is clear then that the nucleus is the most important structure in sexual reproduction, at least so far as the male cell is concerned.

Further consideration of the process shows that in the lower forms, where the union is that of whole cells, it is not merely the cytoplasm but also the nuclei that unite. The latter is the case also in the higher forms. Sexual reproduction, then, is not merely the union of cells, or the entry of a male nucleus into a female cell, but the union of the two nuclei.

But this union of cells and nuclei is not all of the process. To reproduce there must be cell division again, whether it be to produce new individuals at once, in the case of one-celled plants or animals, or to produce the many cells of which the new individual consists, in the case of the many-celled plants and animals.

It will be necessary to review hastily the process of cell and nuclear division in order to understand more clearly what effect the union of nuclei has on the subsequent process.

In its essentials the mitotic division of the cell consists of the division of all elements of the protoplasm into like halves, and the regeneration by each half so formed of the missing half. This latter point is as important as the former. Thus the cytoplasm divides into two masses of cytoplasm, the plastids, in many cases at least, into two plastids each, etc. This division occurs either through cleavage due to the formation of vacuoles between the two halves-to-be or through a drawing apart of the two halves and gradual pinching off as happens when a drop of glue drops from a stick or other object.

The nucleus is not a simple drop of slightly different protoplasm but is more complicated in its structure and accordingly in its mode of division, although it conforms to the rules formulated above. It is a vacuole (nuclear sap) surrounded by a thin, tough membrane (nuclear membrane, which is a part of the cytoplasm) with a tangled thread suspended in the vacuole. On the thread, which may have cross connections from one loop to the next, there are irregular lumps of a highly staining protoplasm particularly at the intersections of the threads. These lumps are made of a substance or substances to which the collective name chromatin is given. There is usually a store of reserve material as a large drop, the nucleolus. This is proteid in nature and is clearly closely related in composition to the chromatin.

Just as the cytoplasm and plastids divide into similar halves so we find division going on within the nucleus. It is, however, only the chromatin lumps that divide. This division occurs in the Myxophyceae where the nucleus is less highly organized than I have described above, apparently by the pulling apart of the chromatin masses. In the better organized nuclei, however, a cleavage plane is produced by the formation of vacuoles which separate the lumps of chromatin into equal halves. This is the essential feature of nuclear division. The matter is not so simple as this statement would make it appear for this cleavage is organized and controlled in a very complicated manner. In brief the process is as follows: the separate chromatin masses crowd together into a definite number of more or less elongated bodies, the chromosomes. Special structures arise in the cytoplasm and entering the nucleus arrange the chromosomes in a definite order and, after they have undergone cleavage, pull apart the halves. These half chromosomes represent merely the crowded together and perhaps partially fused halves of the chromatin lumps of the resting nucleus. As all protoplasm has the power of regenerating itself so each lump regenerates itself exactly (probably using up the food previously stored up in the nucleolus for the purpose) and then the lumps separate and the daughter nuclei are reorganized.

Careful study of a great many animals and plants by investigators in all parts of the world makes it clear that the chromatin lumps always crowd together into the same number of chromosomes, at each nuclear division for the same species of organism. These chromosomes, too, often have characteristic shapes and sizes which are constant for the species. It seems probable that not only are the shape and size of the individual chromosomes constant, but even the relative position in the nucleus. This forces us to the inevitable conclusion that the individual lumps of chromatin which are united into the chromosomes are themselves permanent cell organs and that the complicated mechanism of mitosis is an arrangement by which the halving and distribution of these chromatin masses to the daughter nuclei is made more certain.

These facts have led biologists to assume that the control of the development and functioning of the cells and consequently the structure and physiological nature of the individual resides in these various chromatin masses, in other words, we speak of them as the "carriers of heredity." The further bearings of this theory need not be mentioned here.

When two nuclei fuse in sexual reproduction we find that the

resulting nucleus contains twice as many chromosomes as each of the gamete nuclei. When such a zygote nucleus divides each chromosome divides in the manner described above, so that each daughter nucleus receives the double number of chromosomes. When we examine the chromosomes carefully in the dividing nuclei of various insects and worms as well as of some plants we find that the chromosomes appear to occur by twos. Thus in forms in which there are in the gametes as many shapes of chromosomes as these are in number we find in the nuclei coming from the division of the zygote nucleus the same number of shapes of chromosomes but each shape represented by two chromosomes. Furthermore, the two of a kind usually lie in close proximity to each other. We must conclude that the corresponding chromosomes are equivalent and that the component lumps of chromatin of which these corresponding chromosomes are composed are also equivalent. Thus the zygote nucleus and its progeny possess two chromatin masses of every kind for every one in the gamete nucleus.

Eventually, however, the time comes for new gametes to be formed. If nothing new were to enter in we would expect these to have double the number of chromosomes that were present in the gametes of the previous generations, so that with each generation the chromosome number would be doubled. Such a heaping up of chromosomes is beautifully prevented by the complicated process known as the reduction division or meiosis. This occurs wherever sexual reproduction is found. By its means the number of chromosomes is reduced again from the "diploid" to the original "haploid" number.

The details of meiosis have not been worked out so completely as to be free from controversy. Indeed, there are several theories which differ radically but which are held by their advocates with great tenacity. In objects so minute it is rather natural that preconceived theories may influence the observations made by even the most open-minded of observers. Strasburger reports an amusing instance of this. Two of the leading advocates of diametrically opposite views as to the course of events in meiosis exchanged their slides and all material upon which they had arrived at their conclusions. Each one, working with the other's slides and material arrived, however, at his own original conclusions.

In general the process seems to be a spinning out of the chromatin masses and the threads on which they are apparently strung into a very slender tangled thread that compacts itself into a tight knot in which occur processes the nature and purpose of

which one can only surmise. Later on the thread shortens and thickens and eventually the chromosomes appear in pairs, those of each pair being so closely united as to give to each pair the appearance of a unit. These double chromosomes are naturally haploid in number as each consists of two chromosomes. In the first of the two divisions that make up meiosis these pairs of chromosomes split into their component whole chromosomes, one of which goes to each daughter nucleus, so that the latter receives the haploid number of whole chromosomes instead of the diploid number of half chromosomes. The second of the two divisions is practically normal.

Although it is usually impossible to distinguish the chromosomes from one another in plant cells this is not true of all plants, while in many animals chromosomes have distinctive shapes and positions. In such organisms it has been possible to observe that at meiosis one of each kind of chromosome goes to each daughter nucleus. Since the pairs of such chromosomes arose by the union of the gamete nuclei it is clear that the distribution of the components of the pairs to the daughter nuclei at meiosis must bring to the nuclei the corresponding chromosomes from the two gametes; i.e., the chromosome of male origin goes to one daughter nucleus and that of female origin to the other. There is no reason to believe however, that all the chromosomes from one gamete go to one daughter nucleus and those from the other gamete to the other nucleus. Rather, it seems probable that the question as to whether a given chromosome goes to one or to the other daughter nucleus is wholly a matter of chance.

We can now take a more comprehensive view of the subject of sexual reproduction. It consists of the union of cells, with the nuclear union as the most important feature. But, in order that the process may be repeated, it involves also the reduction of the diploid to the haploid number of chromosomes. This series of events, then, the union of cells, the nuclear union and the reduction division form the sequence of processes that I call the Sexual Cycle.

Whatever group of plants or animals we study we find that the sequence of events remains the same for the sexual cycle. On the other hand there is the greatest variability as to the time intervening between these different cardinal points of the cycle.

In most animals (at least in most Metazoa) the nuclei of the somatic cells are diploid in character. Reduction division does not occur until those cell divisions that produce the gametes (eggs

and sperms). The union of the gametes gives rise to a zygote with a diploid nucleus, the subsequent nuclei all being diploid until meiosis occurs at gamete production again. The sperm mother cell possesses a diploid nucleus. By meiotic division it produces four haploid nuclei, one for each of the four sperms. Within the ovary or after it leaves the ovary the egg mother cell also has a diploid nucleus. The so-called "maturation" divisions that it makes are in reality meiotic and the result is four eggs, of which only one is functional, the other three being the polar bodies. (It must be noted that frequently the first polar body does not divide again, in which case only two polar bodies are apparent.)

Illustrating the sexual cycle schematically as a circle (Fig. 3) we have CU representing the union of the gametes and NU the immediately following nuclear union. The portion of the circle around to the letters RD (reduction division) represents the long stage of somatic development in which nuclear and cell divisions occur until the reduction divisions take place at the time of forming the next generation of gametes.

Turning now to the Vegetable Kingdom we find that there is no such general uniformity of the sexual cycle as we find in animals. The gaps between the different events of the cycle may occur between any two, or there may be two gaps. It will be understood that these "gaps" represent series of nuclear and cell generations between one point of the cycle and the next.

To find a sexual cycle of the type that is prevalent in animals we must turn to *Fucus* (Fig. 3). Here the gametes (produced at

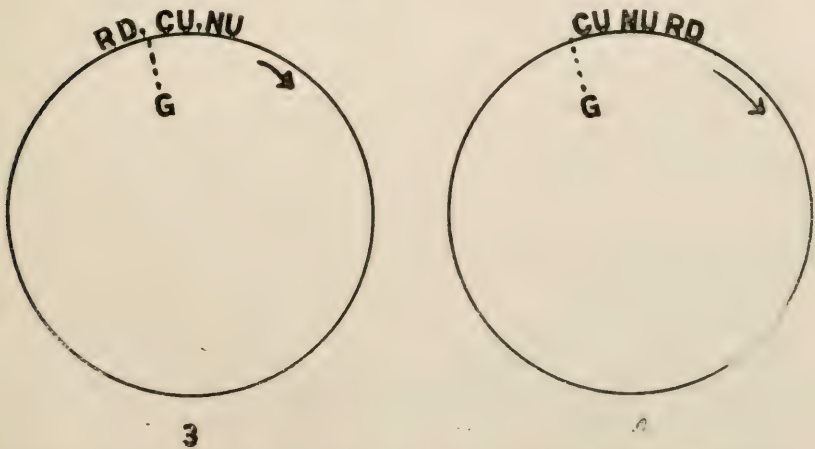


Figure 3. Sexual cycle in Metazoa and in *Fucus*. RD= Reduction division, CU=Cell union, NU=Nuclear union, G=Point of gamete formation.

Figure 4. Probable sexual cycle of *Ulothrix*, *Oedogonium*, *Desmidiaceae*, *Spirogyra*, etc.

the point in the cycle indicated by G) produce a diploid zygote which develops into the plant body without any meiotic division until the eggs and sperms are produced. Thus the three events of the cycle occur in immediate proximity in the order RD, CU, NU.

In *Ulothrix* and *Oedogonium* and a number of other Chlorophyceae the life history includes the production of gametes, their union to zygospores or oospores, and the germination of these, after a longer or shorter period, by the division of the nucleus into four nuclei and the production of four zoospores, each of which produces a new plant. (In *Ulothrix* according to Klebs, these four cells may possibly lack motility). If conjugation is prevented the gametes of *Ulothrix* are capable of developing parthenogenetically. These facts lead to the assumption (which ought to be tested by cytological investigations) that the vegetative cells and the gametes of these plants are haploid. That being the case the ability of the gametes to grow without conjugation would not seem strange. The division of the zygote into four cells is probably accompanied by the meiotic divisions of the nucleus. The sexual cycle would then be illustrated by a diagram (Fig. 4) in which the events are in the order, CU, NU, RD with the main part of the cycle in the haploid condition.

It is probable that the Desmids and Pond Scums (*Zygnematales*) are of this same type, for we find the zygote dividing into four cells in *Mesotaenia* or into two cells with two nuclei each (and one of these two disintegrating) in most Desmids, or, as in *Spirogyra*, with the zygote nucleus dividing into four nuclei, with only one finally functioning further. It seems almost certain that the reduction divisions must occur at this point, but here, too, the matter needs further investigation.

In the higher algae we find that in the Florideae the sexual cycle shows another modification. (Fig. 5). In the majority of this class two generations are distinguishable, the sexual and the tetrasporic. The zygote nucleus divides by ordinary mitotic divisions and is seen to be diploid. The resulting nuclei may invade other cells or not, but eventually enter the threads that give rise terminally to the carpospores. These are also diploid as are the cells of the tetrasporic plant arising from them. It is worthy of note that this generation with the diploid nuclei consists of plants as a general rule much larger than the haploid sexual plants of the same age.*

*A similar difference in size exists between *Oenothera lamarckiana* and one of its mutants, *Oe. gigas* and it is worthy of note that the latter has double the number of chromosomes possessed by the former.

Certain cells of these diploid, tetrasporic plants enlarge and their nuclei undergo meiotic division producing the four nuclei of the four tetraspores, each of which in turn may produce a new sexual plant.

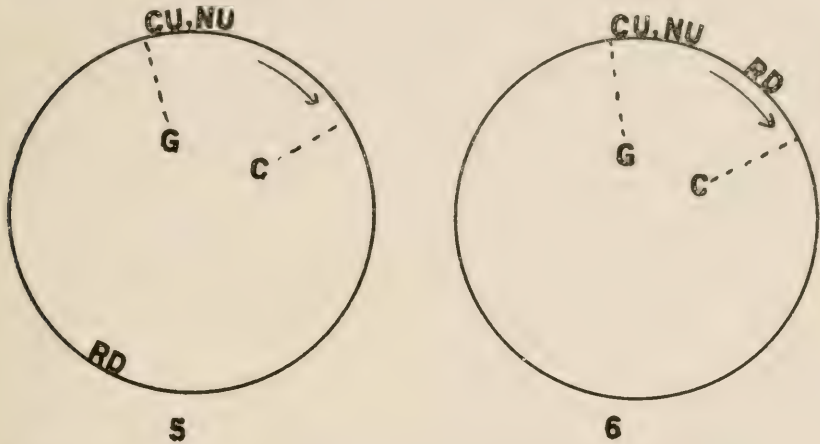


Figure 5. Sexual cycle of such Florideae as possess a distinct tetrasporic generation. C== Point at which carpospores are formed.

Figure 6. Sexual cycle of *Nemalion*.

In the life cycle of these plants we find a large number of nuclear and cell generations occurring between the nuclear union (NU) and reduction division (RD) and again between the latter and the formation and union of the gametes, this being illustrated in the figure.

In some of the Florideae, e. g., *Nemalion*, there is no tetrasporic generation and the carpospores possess haploid nuclei (Fig. 6). Wolf has shown for these that the zygote nuclei and those first entering into the threads which produce the carpospores are diploid, but that the chromosome number becomes reduced somewhere along the course of this thread so that the last division which produces the carpospores shows the nucleus to be haploid. Thus in the rather closely related plants represented on the one hand by *Nemalion* and on the other, for example by *Polysiphonia*, the reduction division precedes the carpospore production or follows long after, respectively.

In the Bryophyta the alternation of generations becomes fairly well marked. In these plants the sexual cycle (Fig. 7) is much like that in *Nemalion* except that the number of cell generations is vastly greater between the zygote and the reduction divisions that take place, just before spore production, in the spore mother

cells. The permanent generation, or the plant body, of the Moss or Liverwort consists of cells with haploid nuclei. The zygote by its division produces the mass of cells with diploid nuclei, some of which remain sterile and have protective or assimilative functions while others become the spore mother cells within which, after meiosis the four nuclei become the spore nuclei. Because in the Ferns this sporogenous structure that arises from the zygote has an independent existence as a distinct generation botanists usually apply the terms gametophyte and sporophyte to the main plant body and the sporogenous structure respectively, of the Bryophyta also.

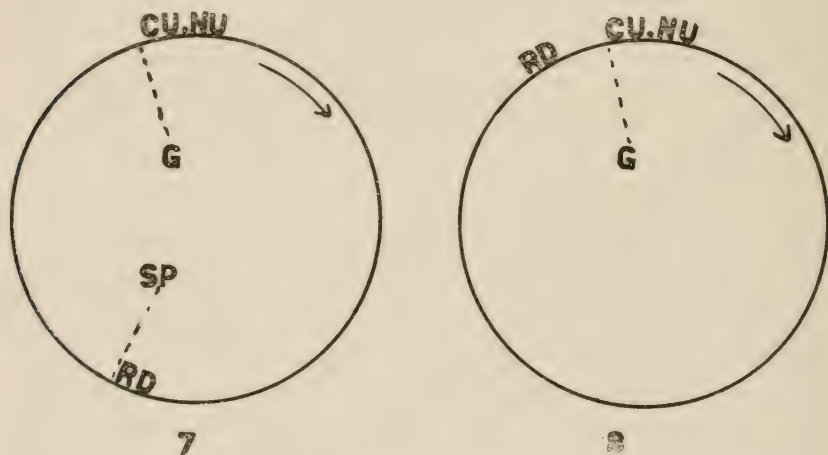


Figure 7. Sexual cycle of Mosses and Ferns. SP=Point of spore production.
Figure 8. Sexual cycle in the Flowering Plants.

In the Ferns the sexual generation, the gametophyte, is the short-lived one, and the sporophyte long-lived. Otherwise the sexual cycle is the same as for the Bryophyta (Fig. 7). Very incorrectly these two generations are often spoken of as the sexual and asexual generations respectively. I have tried to point out that the re-reduction division is as important part of the sexual cycle as the cell and nuclear union. The sporophyte is merely a further development of the comparatively few-celled structure that arises from the zygote in Nemalion and produces the carpospores: (I do not want to be misunderstood as holding that Nemalion is a direct ancestor of the Ferns or Mosses, but I mean that a further development of the same idea that appears in Nemalion gave rise to the sporophyte in these groups). The true asexual reproduction is that by which the same generation is perpetuated, not that repro-

duction that is the complement of the cell union. Thus the formation of gemmae on the liverwort gametophyte or of the bulbils on the sporophytes of certain ferns is true asexual reproduction. The formation of spores in the moss capsule, on the other hand, is merely the final stage of the sexual reproduction begun by the union of sperm and egg in the archegone.

The fern type of sexual cycle persists in the still higher plants with a shoving of reduction division (RD) further and further towards the point of gamete production (G). Finally in the Anthophyta (the flowering plants proper, as distinguished from the Gymnosperms), the haploid stage represents only two nuclear generations in the male gametophyte and three (sometimes less) in the female gametophyte. (Fig. 8.) Thus in a very different group of plants we come back to almost the same style of sexual cycle that occurs in *Fucus*, the prevalent animal type.

In all of the examples that have been mentioned the cell union has been followed immediately by the nuclear union. This is not always the case in plants. In the Ascomyceteae, Claussen worked out the cytological details from the time of entry of the male nuclei into the oogone up to the formation of the ascospores. The main points are as follows: Upon the union of the club-shaped antherid with the trichogyne of the oogone the numerous male nuclei pass from the former into the latter and then into the oogone proper. Here the male nuclei approach but do not unite with the female nuclei. They arrange themselves in pairs and divide simultaneously. By this "conjugate" division numerous pairs of nuclei are produced and these migrate out into the ascogenous hyphae. In these eventually cross walls are laid down so that each cell contains two nuclei, one probably descended from a male nucleus and the other from a female nucleus. Finally at the extremity of each ascogenous hypha the two nuclei unite, forming the single, diploid, nucleus of the young ascus. This divides now by reduction division so that the ascus soon contains four haploid nuclei. Another vegetative division of the nuclei produces the eight nuclei, the number normal to this plant. About each is formed an ascospore. These ascospores produce the new plants. In the whole life history of the plant there is but one diploid nucleus, the one formed in the young ascus by the union of the two nuclei of respectively male and female ancestry. The threads that bear the asci, the ascogenous hyphae, contain in their cells two nuclei, but these are haploid. The cells of the vegetative mycelium have only haploid nuclei. We must note, however, that the *cells* of the asco-

genous hyphae are diploid even though the two nuclei in each cell are haploid, for so far as the functions of the cells are concerned there can be little difference whether the two sets of chromosomes, respectively of the male and female origin, are enclosed in one common nuclear membrane or in two separate membranes.

The sexual cycle (Fig. 9) may be represented graphically with a moderate gap between the point of cell union (CU) and that of nuclear union (NU), this gap representing the nuclear generations during which the nuclei are in pairs and division is conjugate. The main vegetable growth, however, lies between RD and CU.

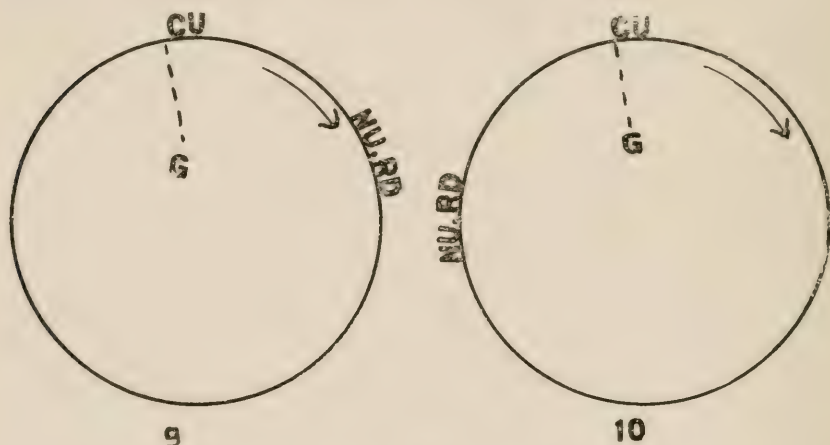


Figure 9. Sexual cycle in *Pyrenopeziza*.
Figure 10. Sexual cycle in the Rusts.

In the Rusts this scheme is still further modified. The cell union occurs in the aecium, giving rise to a chain of binucleate aeciospores. These produce on the same or a different host a mycelium all of whose cells are binucleate. Secondary, truly asexual spores, the urediniospores, may occur to multiply this stage. Finally, however, binucleate teliospores are formed. The two nuclei fuse and a diploid nucleus is formed; like that of the young ascus the only one in the life history of the rusts. When this nucleus divides it is by a reduction division to form the four nuclei of the promycelium and so the nuclei of the uninucleate sporidia. The mycelium produced by these consists of uninucleate cells. It is on this mycelium that arise the hyphae which by their union in the aecium begin the binucleate stage again.

Here as in the Ascomyceteae there exists a stage with binucleate cells and one with uninucleate cells, but the former is usually

the longer. Furthermore, it is completely independent of the uninucleate stage and not dependent upon it as in the Ascomyceteae. Its cells are essentially diploid for they contain two nuclei (respectively male and female) but each nucleus is haploid. The diagram (Fig. 10) shows the stage between cell union in the aecium (CU) and nuclear union in the teliospore (NU) as considerably longer than the stage from reduction division (RD) and sporidial formation to cell union (CU).

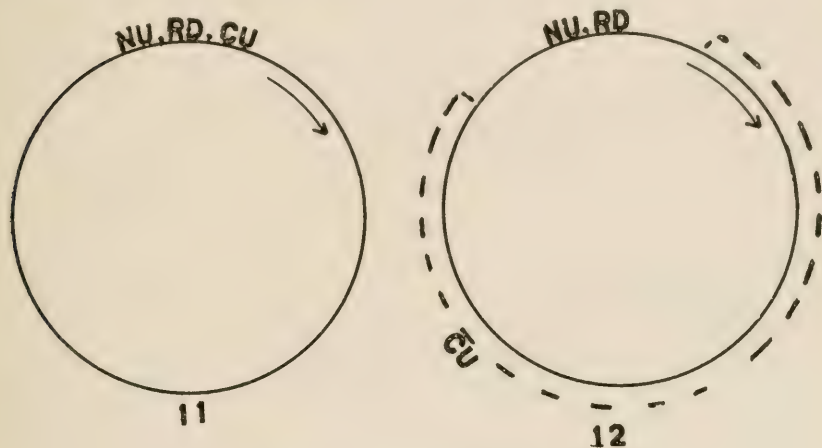


Figure 11. Sexual cycle in *Tilletia*.
Figure 12. Sexual cycle in Agaricales.

In the genus *Tilletia* (Fig. 11) the binucleate stage is extended to its fullest extent. Here the vegetative mycelium for the whole life history of the fungus consists of binucleate cells. At the time of spore formation the young spores are binucleate but the nuclei unite so that the only diploid nucleus of the life history is formed. A promycelium is formed and within it takes place in all probability the reduction division so that the nuclei of the sporidia are haploid again. The sporidia almost invariably conjugate even before becoming detached from the promycelium, the nucleus from one passing into the other sporidium but with no nuclear fusion. The germ tube from this binucleate sporidium has its nuclei two to each cell. Here we have the three main events of the sexual cycle in immediate succession, nuclear union in the spore, reduction division in the promycelium and cell union in the sporidia, with the whole vegetative mycelium possessing two nuclei to a cell.

Finally we must look at the Agaricales in which the point at

which the mycelium becomes binucleate is very variable. In some species the single nucleus of the basidiospore divides, so that from that point on every cell of the mycelium is binucleate, the nuclear union taking place in the basidium, to be followed immediately by reduction division so that the nuclei of the usually four basidiospores are haploid. In other cases, however, the basidiospores remain uninucleate and the vegetative mycelium possess but one nucleus to the cell. Somewhere, however, before the hymenium is formed the cells become binucleate, apparently by the omission of a septum after nuclear division, rather than by a true union. This is so variable that I have had to indicate (Fig. 12) by a dotted line the fact that the point where the cells become binucleate (and which correspond to the point of cell union) is not fixed.

Reviewing now the different sexual cycles that have been illustrated, it will be noted that they all agree in the order of their events, i. e., cell union, nuclear union and reduction division. But these events are seen to be like movable balls on a wire ring. They can be arranged in almost any position, in close proximity by threes or by twos or scattered, but they cannot be passed by one another. Thus we have them in threes in the three possible combinations: RD, CU, NU in *Fucus*, CU, NU, RD in *Ulothrix* and *Oedogonium*, NU, RD, CU, in *Tilletia*; or by twos with the third removed to some more distant point in the cycle as CU, NU in *Floridaceae* and *Mosses*, NU, RD in *Ascomyceteae* and many other fungi. The arrangement with all three items scattered evenly on the cycle is, however, not known.

We may for a little consider the bearing of the foregoing upon alternation of generations as well as the effect of apogamy or parthenogenesis upon the cycle.

Strasburger was very insistent that the sporophyte always began with the zygote and the gametophyte with the haploid cells produced in the course of reduction division, and refused to consider as homologous two structures of similar morphological origin if one contained haploid and the other diploid nuclei. Thus the carpophores of *Nemalion* are, following Strasburger, considered by some as entirely lacking homology with those of *Polysiphonia*, in spite of the fact that they are produced in the same manner, morphologically. The plant body of *Fucus* is called by such botanists a sporophyte in spite of the fact that it bears the antherids and oogone. Is this right? I believe not.

It is in the determination of this question that the cytological studies of apogamous plants have thrown much light. Take the

case of *Aspidium falcatum*, one of the ferns. For several decades it had been known that the sporophyte developed from the proliferation of the cells of the gametophyte, not from a fertilized egg. The gametophyte produces antherids with normal sperms but the archegones degenerate before the eggs reach maturity so that the latter are never fertilized and in fact never function at all. On the sporophyte are produced typical sporangia within which spores are produced which give rise to the new gametophyte. It has been known for some years that spore production within the fern sporangium is typically brought about by the formation of four spores each in usually sixteen spore mother cells, the nuclear divisions being in the nature of reduction divisions. Manifestly reduction divisions cannot continue to occur at each generation unless there is a nuclear union somewhere, and this is entirely lacking in the gametophyte.

Miss R. F. Allen, accordingly took up this point and investigated the development of the sperms and of the sporangia of the gametophyte and sporophyte respectively. She determined the chromosome number in the gametophyte to be between 60 and 65, with perfectly normal development of the sperms. The sporophyte also had the same chromosome number, a confirmation of the previous observations in which no cell union had been observed. In the sporangia there appeared sixteen cells exactly like the sixteen spore mother cells of normal fern. These, however, united by pairs with complete fusion of both cells and nuclei, thus producing eight cells with diploid nuclei. Each now acted like a normal spore mother cell and its nucleus underwent reduction division and four spores were formed in each cell; thirty-two for the sporangium instead of sixty-four as for normal ferns.

It is manifestly entirely improper to call the leafy plant on which the sporangia were borne a gametophyte because of retaining the haploid number of chromosomes in its nuclei. If that is done then the sporophyte is only one-celled, for at only one stage is the nucleus diploid, i. e., just after the fusion of the two spore mother cells.

Miss Allen calls attention to cases where the gametophyte retains the diploid number of chromosomes, as in some apogamous flowering plants, e. g., *Antennaria*, *Hieracium*, *Thalictrum*, in which the embryo sac arises without a preceding reduction division although this may be present in pollen production. In such embryo sacs the egg develops apogamously. In certain cultivated varieties of ferns fertilization and development are normal; in closely related

varieties of the same species the sporophyte arises apogamously from the gametophyte, and the latter aposporously from the sporangial sorus of the sporophyte, both generations retaining the chromosome number equal to the diploid number in the closely related normal plant.

In view of these facts elucidated from the apogamous ferns and flowering plants and of the extreme variability of the position of the main points of the sexual cycle in different plants it seems far more reasonable to me to distinguish sporophyte and gametophyte on morphological grounds and to be willing to homologize structures even when the chromosomes are diploid in number in the one and haploid in the other. This would permit the structure arising from the zygote in *Coleochaete* to be homologized with the sporophyte of the liverwort, a much needed homology in phylogenetic speculation.

One thing remains clear, however. The retention of the reduction division seems to demand a sexual union somewhere. If this can be in the normal way, well and good, if this is prevented there must be a substitution union elsewhere. Thus in *Aspidium falcatum* when the gametophyte buds off into a sporophyte, thus eliminating the normal union, the sexual union is replaced by the union of spore mother cells in the sporangium. In one species of *Pyronema* studied by Brown in which the antherid and trichogyne do not fuse the place of the male nuclei is taken by other female nuclei already present in the oogone. In the rusts the pycniospores are almost certainly sperm cells, but they never have a chance to function so that their place is taken by cells adjacent to the oogones, probably modified oogones themselves.

One further point, too, is clear. Just as the point of cell and nuclear union is not absolutely fixed so the point of reduction division is movable. In *Nemalion* it is shortly after nuclear union and before carpospore formation, in *Polysiphonia* it is after carpospore formation at the close of the tetraspore stage. In *Fucus* it is at the close of the vegetative growth at gamete production (as in animals) in *Ulothrix* probably at the germination of the zygospore.

I shall not undertake to show why this is so or what is the purpose of sexual reproduction. I have merely attempted to show some of the features connected with this subject.

Department of Botany, Michigan Agricultural College, East Lansing.

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FERN NOTES.

BY OLIVER ATKINS FARWELL.

During the past few years as a result of researches in field, herbarium, and library, a number of interesting discoveries and novelties have been brought to light and this paper puts on record some of the results and conclusions arrived at during the course of these studies.

POLYPODIALES.

POLYPODIACEAE.

Pteris aquilina, Linne var. *Pseudocaudata*, Clute.

This is a form of the species in which many of the pinnules are *narrow*, *entire*, and *elongated*, particularly the terminal ones. It is only rarely met with. I have found it at Detroit, No. 3516½, August 10, 1913, in sterile or sandy situations; also on sandy hills at Rochester, No. 2560½, July 14, 1912.

Asplenium pinnatifidum, Nutt.

I have never seen this species in the field but in my herbarium I have a sheet showing several plants which were collected at Cobden, Illinois, by Mr. M. B. Waite, June 8, 1885. These, with the exception of one plant, are normal *A. pinnatifidum*; the one abnormal plant is normal in all respects except segmentation which is exactly that of *A. ebenoides*, R. R. Scott, i. e., the lobes are lanceolate and acute instead of round-ovate and obtuse, and of variable lengths, short and long lobes often alternating. If *A. ebenoides* is a hybrid between *Camptosorus rhizophyllus* and *Asplenium platyneuron* with a trend toward the latter parent, why may not *A. pinnatifidum* be a similar hybrid with a tendency toward the former parent? This peculiar plant would seem to so indicate.

Asplenium platyneuron (Linne) Oakes.

A rare fern in Michigan. Beal, in the Michigan Flora, states that Allegan is the only station in the State. I found it at Williamstown, Ingham Co., May 28, 1905, No. 1903.

Athyrium Felix-femina (Linne) Roth.

There is a wide degree of variation in the pinnation and size of the different forms that have been referred to this species; the

extremes have been variously regarded as synonymous with the typical form, as varieties of it, or as distinct species. Since the indusial characters, texture of fronds, and general appearance is much the same in all the forms the happiest medium probably will be best served by considering them all as varieties of one species. In addition to the type the following varieties are found in Michigan.

ATHYRIUM FILIX-FEMINA var. *MICHAUXII* (Spreng.), N. Comb.

Aspidium angustum Willd., Sp. Pl., 5, 277, 1810.

Asplenium Michauxii Spreng., Syst. 4, 88, 1827.

Asplenium Filix-femina var. *Michauxii* Mett., Fil. Hort. Lips., 79, 1856.

Athyrium asplenoides var. *angustum* Moore, Index, 179, 1860.

Asplenium Filix-femina var. *angustum* D. C. E. Ferns of the South-west. 330, 1878.

Athyrium Filix-femina var. *angustum* (Willd.) Farwell, Mich. Acad. Sci., 6, 201, 1904.

Keweenaw Co., No. 757, July 18, 1890. Frequent in rocky situations. Parkedale Farm, No. 3039 a, August 4, 1912. Frequent in dry thickets.

Athyrium Filix-femina var. *multidentatum* (Döll) Milde, Fil. Eur., 50, 1867.

Asplenium Filix-femina var. *multidentatum* Döll, Rhein. Fl., 12, 1843.

Athyrium Filix-femina var. *cyclosorum* (Ruprecht) Moore, Index., 183, 1860.

The largest and most divided form. Keweenaw Co., No. 502. July 28, 1887 in moist thickets; common. Detroit, No. 502 a, Oct. 16, 1910, in moist thickets; common.

Athyrium Filix-femina var. *latifolium*, Moore, Nat. Pr. Brit. Fer. tr. 31B, 1855, Keweenaw county; No. 590, Sept. 5, 1887 in rocky or sterile situations, frequent.

FILIX (Fuchs) Hill, Family Herbal 171, 1755.

Dryopteris Adanson, Fam. Pl. 2, 20 and 550, 1763.

Aspidium Swartz, Schrad. Journ. Bot. 1800, 2, 29, 1801.

Nephrodium Rich., Cat. Jard. Med. Par. 120, 1801.

Lastrea Bory, Diet. Class. d'Hist. Nat. 6, 588, 1824.

Underwood and others have adopted *Filix*, Adanson, (1763) as the oldest post Linnaean name for those ferns that generally have been known under the name of *Cystopteris*, Bernhardt (1806). According to Christensen, Ludwig used the name *Filix* in 1757, perhaps in the same sense. Hill, however, in the Family Herbal

used it for the Male Fern and the Female Fern. I will quote a few lines from the preface of this volume in order to show the attitude at that time of Sir John Hill, toward botanical science as well as to show that he intended the volume to be of a botanical nature as well as a medical dispensatory.

"It grieves a man of public spirit and humanity, to see those things which are the means alone of the advantages of mankind studied, while in the end that advantage itself is forgotten. And in this view he will regard a Culpepper as a more respectable person than a Linnaeus or a Dillemius." "That Botany is an useful study is plain; because it is in vain that we know betony is good for headaches, or self-heal for wounds, unless we can distinguish betony and self-heal from one another, and so it runs through the whole study."

"We are taught by it to know what plants belong to what names, and to know that very distinctly; and we shall be prevented by that knowledge from giving a purge for an astringent, a poison for a remedy; let us therefore esteem the study of botany, but let us know, that this use of the distinctions it gives is the true end of it; and let us respect those, who employ their lives in establishing those distinctions upon the most certain foundations, upon making them the most accurately, and carrying them the farthest possible; these are the botanists; but with all the gratitude we owe them for their labours, and all the respect we show them on that consideration, let us understand them as but the seconds in this science. The principal are those who know how to bring their discoveries to use, and can say what are the ends that will be answered by those plants, which they have so accurately distinguished."

"The plants are arranged according to the English alphabet, that the English reader may know where to find them: they are called by one name only in English, and one in Latin; and these are their most familiar names in those languages; no matter what Casper or John Bauhine, or Linnaeus call them, they are here set down by those names by which every one speaks of them in English; and the Latin name is added, under which they will be found in every dictionary. To this is subjoined a general description of the plant, if it be a common one, in a line of two; that those who already know it, may turn at once to the uses; and for such as do not, a further and more particular account is added."

There is, then, no doubt that he intended the work to be botanical, as well as useful from a therapeutic point of view, and it can

not, therefore, be ignored any more than other volumes of a botanical nature. The latin names are either uninomials, binomials, or polynomials. The work contains no generic descriptions as such but the Latin names are accompanied by descriptions supplemented, in some instances, by illustrations, so that there is no question as to the identity of the plant described, thus making the publication effective according to Article 35 of the Vienna Code. On pages 171 & 172, in the order given herewith, Hill described two species; Male Fern, *Filix mas* and Female Fern, *Filix Foemina*. The male Fern is the species known as such at the present time. The Female Fern is the one that was published by Linne as *Pteris aquilina*. The names *Filix mas* and *Filix foemina* as here used by Hill must be considered as true binomials and not in any sense as generic names as employed by him a year later in the British Herbal. Since the binomial has been effectively published it follows that each element of the binomial, that is to say, that the generic name and the specific name each has been effectively published and the proper citation for the genus is *Filix* (Fuchs) Hill, Family Herbal 171, 1755.

The North America species not already transferred are as follows:

- FILIX AMPLA* (H. & B.) N. Comb.
Polypodium amplum H. & B. ex Willd., Sp. Pl., 5, 207, 1810.
FILIX AQUILONARIS (Maxon), N. Comb.
Dryopteris aquilonaris Maxon, Bul. Tor. Bot. Cl., 27, 638, 1900.
FILIX BOOTHII (Tuckerm.), N. Comb.
Aspidium Boothii Tuckerm., Hovey's Magazine, 9, 145, 1843.
FILIX CRISTATA (Linne), N. Comb.
Polypodium cristatum Linne, Sp. Pl., 1090, 1753.
FILIX CRISTATA var. *CLINTONIANA* (D. C. E.), N. Comb.
Aspidium cristatum var. *Clintonianum* D. C. E. in Gr. Man., Ed. 5, 665, 1867.
FILIX FLORIDANA (Hook), N. Comb.
Nephrodium Floridanum Hooker, Fil. Exot., t. 99, 1859.
FILIX FRAGRANS (Linne), N. Comb.
Polypodium fragrans Linne, Sp. Pl., 1089, 1753.
FILIX GOGGILODES (Schk.), N. Comb.
Nephrodium unitum R. Br., non Sieb., nor *Polypodium unitum* Lin., Syst. Nat., X., 2, 1326, 1759.
Aspidium goggilodus Schk., Kr. Gew., 1, 193, t. 33c, 1809.
FILIX GOLDIANA (Hooker), N. Comb.
Aspidium Goldianum Hooker, Edinb. Philos. Journ., 6, 333, 1822.

FILIX GOLDIANA var. CELSA (Palmer), N. Comb.

Dryopteris Goldiana celsa Palmer, Proc. Biol. Soc. Wash., 13, 65, 1899.

FILIX MARGINALIS (Linne), N. Comb.

Polypodium marginale Linne, Sp. Pl., 1091, 1753.

FILIX MARGINALIS var. BIPINNATIFIDA (Clute), N. Comb.

Nephrodium marginale f. bipinnatifidum Clute, Fern Bul. 19, 50, 1911.

In woods at Detroit No. 1652, August 22, 1899, rare. This fern has the general appearance of *F. spinulosa* var. *Americana* but it is not spinulose and the sori are marginal. It apparently is the same thing described by Clute as *Nephrodium marginale forma bipinnatifidum*. It may be one of the so-called fern hybrids with *Filix marginalis* and *F. spinulosa* var. *Americana* as the parents.

FILIX MONTANA (Vogler), N. Comb.

Polypodium montanum Volger, Dissert, 1781.

Polypodium oreopteris Ehrh. ex. Willd., Prod., 292, 1787.

FILIX NOVEBORACENSIS (Linne), N. Comb.

Polypodium Noveboracense Linne, Sp. Pl., 1091, 1753.

FILIX OPPOSITA (Vahl), (*Polypodium oppositum* Vahl, Ecl. Amer., 3, 53, 1807) var. *strigosa* (Fee), N. Comb.

Aspidium strigosum Fee, 11 MeM., 78, t. 22, f. 2, 1866.

Dryopteris contermina strigosa (Fee) Underwood.

FILIX OREGANA (C. Chr.), N. Comb.

Dryopteris Oregana C. Chr., Ind. Fil., 281, 1905.

FILIX PARASITICA (Linne), N. Comb.

Polypodium parasiticum Linne, Sp. Pl., 1090, 1753.

FILIX PATENS (Swartz), N. Comb.

Polypodium patens Swz., Prod., 133, 1788.

FILIX PATENS var. STIPULARIS (Willd.), N. Comb.

Aspidium stipulare Willd., Sp. Pl., 5, 239, 1810.

FILIX PATULA (Swartz), N. Comb.

Aspidium patulum Swz., Vet. Ak. Hdl., (1817) 64.

FILIX RIGIDA (Hoffm.) (*Polypodium rigidum* Hoffm., Deutsch. Fl., 2, 6, 1795) var. *arguta* (Klf.), N. Comb.

Aspidium argutum Klf., Enum., 242, 1824.

FILIX SETIGERA (Blume), N. Comb.

Cheilanthes setigera Blume, Enum., 138, 1828.

FILIX SPINULOSA (Muell.) Farwell var. *AMERICANA* (Fischer), N. Comb.

Aspidium spinulosum Americanum Fischer ex. Kunz, Amer. Jour. Sci., Ser. 2, 6, 84, 1848.

FILIX SPINULOSA var. CONCORDIANA (Davenp.), N. Comb.

Dryopteris spinulosa (Muell.) Swz. var. *Concordiana* (Davenp.) Eastman, New England Ferns, 1904, and in Gray's New Man., 43, 1908.

FILIX SPINULOSA var. DILATATA (Hoff.), N. Comb.

Polypodium dilatatum Hoff., Deutsch. Fl., 2, 7, 1795.

The *F. spinulosa* var. *dilatata* Farwell, Mich. Acad. Sci., 6, 209, 1904, is the var. *Americana*.

FILIX SPINULOSA var. INTERMEDIA (Muhl.), N. Comb.

Polypodium intermedium Muhl. ex Willd., Sp. Pl., 5, 262, 1810.

FILIX SPINULOSA var. PITTSFORDENSIS (Slosson), N. Comb.

Dryopteris Pittsfordensis Slosson, Rhodera, 6, 75, 1904.

Cystopteris Filix-fragilis (Lin.) Chiovenda.

A common fern in rocky woods. Besides the typical form three others are frequently met with.

CYSTOPTERIS FILIX-FRAGILIS var. LOBULATO-DENTATA (Koch), N. Comb.

C. fragilis var. *lobulato-dentata* Koch., Syn., Ed. 2, 980, 1845.

C. fragilis var. *dentata* Hooker, Sp. Fil., I, 198, 1846.

C. Filix-fragilis var. *tenuis* (Mx.) Farwell, Mich. Acad. Sci., 6, 200, 1904.

The earliest varietal name is that of Koch.

Keweenaw Co., No. 830, August 30, 1890, in rocky woods. Frequent. Ypsilanti, No. 830a, June 11, 1892, in moist woods.

CYSTOPTERIS FILIX-FRAGILIS var. ANGUSTATA (Hoff.), N. Comb.

Polypodium fragilis var. *angustatum* Hoff., Roem. et Uster. Mag., IX, Pt. 11, t. I, Fig. 14d, 1790.

C. fragilis subvar. *angustata* Koch. Syn., Ed. 2, 980, 1845.

C. fragilis var. *angustata* Luerssen, Farnpfl, 459, 1889.

Keweenaw Co., No. 405½, July 8, 1886, in rocky woods; frequent.

CYSTOPTERIS FILIX-FRAGILIS var. LACINIATA (Davenp.), N. Comb.

C. fragilis var. *laciniata* Davenp. in D. C. E., Ferns of N. Amer., 2, 52, 1880.

Keweenaw Co., No. 830½, August 30, 1890, in rocky woods; rare.

These forms or varieties are well illustrated on Plate 53 of Eaton's Ferns of N. America.

OPHIOGLOSSACEAE.

Ophioglossum vulgatum, Lin.

A variable species which, taken as a whole, has an equally variable habitat. I have found it in Keweenaw Co., but it is not frequent even when met with. The typical species has a sessile sterile

frond near the middle of the stem, about equalling the fertile segment, or sometimes a little longer or a little shorter. No. 584½, Sept. 5, 1887, in moist, sandy places along the borders of shallow streams.

Ophioglossum vulgatum var. *pseudopodium* (Blake), N. Comb.

Ophioglossum vulgatum forma *Pseudopodium* Blake, Rhodora, 15, 87, 1913.

A larger plant than the species, the sterile frond more ovate, $\frac{1}{2}$ to $1\frac{1}{4}$ inches wide by 3 to 5 inches long, and tapering into a petiole like base. No. 584, Sept. 5, 1887, in wet meadow lands with more or less sphagnum and other mosses.

Ophioglossum vulgatum var. *minus*, Moore.

This is the slenderest form of the species as found in Keweenaw Co. The sterile blade is small ($\frac{1}{4}$ to $\frac{5}{8}$ inch wide by $\frac{3}{4}$ to $1\frac{3}{8}$ inches long) ovate or elliptic, sessile near the base of the stalk and far overtopped by the fertile segment, the whole plant about 5 inches in height. No. 585, Sept. 5, 1887, on sterile hillsides covered with a sparse growth of grasses and sedges. The whole plant is yellowish while that of the other two varieties is green. Undoubtedly this plant belongs here but it is the one that has been reported in Beal's Flora of Michigan as *O. Engelmanni*.

Botrychium lunaria var. *onondagense* (Underwood), N. Comb.

Botrychium Onondagense Underwood, Bul. Torr. Bot. Cl., 30, 47, 1903.

No. 1787, August, 1902, at Copper Harbor in oak and maple woods. Rare. Forms are found which are intermediate between *B. lunaria*, and *B. Onondagense* indicating that the latter is only an extreme form and therefore is better considered as a variety of the former.

Botrychium lanceolatum var. *angustisegmentum*, Pease and Moore.

The plant listed in Beal's Flora of Michigan as *Botrychium lanceolatum* is the one recently described as the variety *angustisegmentum* by Pease and Moore. It grows with *B. Matricariaefolium* and other forms appear to be intermediate and to intergrade into either; further study may show that it is not specifically distinct from *B. Matricariaefolium*. No. 588, Sept. 5, 1887; usually in mould under hazel bushes, etc., but sometimes in grassy places in the open.

Botrychium Matricariaefolium, A. Br.

It has been very conclusively shown that the *Osmunda ramosa*, Roth, is not this species and that when Ascherson transferred Roth's

specific name to it, it was through a misidentification and resulted in a misapplication of the name. The American plant can not be considered as specifically different from that of Europe. The sterile frond is extremely variable as to the degree of dissection and this fact has led to the description and naming of several varieties or species based on the degree of division of the sterile lamina. It is a very common fern in Keweenaw Co., delighting mostly in a rich humus, consisting of moulding and decaying leaves, underneath deciduous shrubs and trees but not disdaining to come out into the open where it may be found in grassy patches when it is almost completely hidden from view. I have seen large colonies of it and almost every form imaginable is to be found in such a colony; this fact alone proves that the various forms are of one and the same species. The typical form has the sterile blade oblong or ovate, simply pinnate with the more or less distant pinnae lobed or pinnatifid, the lowest pair somewhat longer than the others. No. 1612a, August 25, 1898, Keweenaw Co.

BOTRYCHIUM MATRICARIAEFOLIUM A. Br. var. *RHOMBEUM* (Angstrom), N. Comb.

Botrychium Lunaria var. *rhombeum* Angstrom, Bot. Not., 70, 1854.

Botrychium Matricariaefolium var. *subintegrum* Milde, Mon. der deutschs. *Ophioglos.* 14, 1856.

Botrychium ramosum var. *neglectum* (Wood) Farwell, Mich. Acad. Sci., 6, 200, 1904.

This is a simple form of the sterile frond which is 1 or 2 inches long, simply pinnate with 3-9 nearly equal, rounded, oval, or oblong, obtuse, pinnae, more or less toothed or incised. No. 618, July 26, 1888, in moist shady woods in Keweenaw Co. No. 2714, June 16, 1912, in open, moist, sandy fields, near Algonac.

Botrychium Matricariaefolium var. *compositum* Milde.

This variety has the lowest pair of pinnae much elongated and pinnate so that the whole frond appears to consist of three subequal and similar divisions. No. 1612, August 22, 1898, in maple and oak woods in Keweenaw Co.

Botrychium dissectum Spreng., Anlejt., 3, 172, 1804.

Botrychium lunarioides var. *dissectum*. A. Gr., Man. Bot., 635, 1848.

Dissectum is the earliest specific name for that group of forms that has been passing as *Botrychium obliquum* and hence Sprengel's name should be restored. The ultimate divisions are ovate or oblonglanceolate, incisely toothed. In moist thickets and fields, Detroit, rare. No. 1975, June 18, 1906.

BOTRYCHIUM DISSECTUM var. *OBLIQUUM* (Muhl.), N. Comb.

Botrychium obliquum Muhl. ex Willd., Sp. Pl., 5, 63, 1810.

Botrychium lunarioides var. *obliquum* A. Gr., Man. Bot., 635, 1848.

The ultimate divisions are crenulate-serrulate. In fields and more frequent than the type. No. 872, October 15, 1895, at Detroit.

BOTRYCHIUM DISSECTUM var. *ELONGATUM* (Gilbert & Harberer), N. Comb.

Botrychium obliquum var. *elongatum* Gilbert & Harberer, Fern Bul., 11, 89, July, 1903.

Ultimate segments lanceolate, elongated, crenulate-serrulate. Occasional, No. 3552½, October 12, 1913, in sandy fields at Algonac.

Botrychium multifidum (Gmel.) Rupr.

Osmunda multifida Gmel., Nov. Comm. Ac. Petr., 12, 517, t. 11, f.1, 1768.

Osmunda Matricariae Schrank, Bair. Flora, 2, 419, 1789.

Botrychium Rutacifolium A. Br. ex. Döll, Rhein. Flora, 24, 1843.

Botrychium ternatum A. *Europaeum* Milde, Fil. Europ., 199, 1867.

Botrychium ternatum var. *Rutacifolium* D. C. E., Fer. N. Amer., 1, 149, 1879.

This species is similar to the last preceding but it is usually larger, more compound in most of its forms, with the ultimate segments ovate or obovate and obtuse. The type is rather a small plant with few, broad ovate, obtuse segments, the lowest subulate. No. 627, July 31, 1888, Keweenaw Co., in moist, sandy places; No. 2715, June 16, 1912, near Algonac.

BOTRYCHIUM MULTIFIDUM var. *ONEIDENSE* (Gilbert), N. Comb.

Botrychium obliquum var. *Oneidense* (Gilbert) Waters in Gray's New Manual, 49, 1908.

The broadly oblong, obtuse, sub-cordate segments of this variety seem to place it with this species rather than with the preceding. Keweenaw Co., No. 854, July 5, 1895, in moist meadows.

BOTRYCHIUM MULTIFIDUM var. *AUSTRALE* (D. C. E.), N. Comb.

Botrychium ternatum var. *australe* D. C. E., Ferns N. Amer., 1, 149, Plate XX a (largest plant), 1879.

Botrychium silaifolium Pr., Rel. Haenk, 1, 76, 1825.

Botrychium occidentale Und., Bul. Torr. Bot. Cl., 25, 538, 1898.

Botrychium obliquum var. *Harbereri* Gilbert.

This is the largest form of the species and many individuals carry the sterile lamina of the preceding year well along into the summer so that it may be gathered in good condition with two sterile

fronds on the same plant. Keweenaw Co., No. 708, Sept. 20, 1888. common in grassy fields and meadows; Rochester, No. 628 a, Aug. 15, 1909.

BOTRYCHIUM MULTIFIDUM VAR. *INTERMEDIUM* (D. C. E.), N. Comb.

Botrychium ternatum subvar. *intermedium* D. C. E., Ferns, N. Amer. 1, 149, Plate XX a (Plant in front), 1879.

Intermediate between the species and the variety *australe*. Fields and meadows, common, Keweenaw Co., No. 628, July 31, 1888.

BOTRYCHIUM MULTIFIDUM VAR. *DICHOTOMUM*, N. Var.

Twice dichotomously branched showing two long, and one short-stalked, fertile segments and one short-stalked sterile lamina. The primary and secondary divisions of the stem are about 1 cm. in length, while the tertiary divisions are of variable lengths. The sterile lamina is small (15 mm. long by 10 mm. wide at the base), ovate, pinnatifid with 5-7 small, closely placed, semi-lunate to obvate, somewhat cuneate, obtuse lobes, entire or denticulate, on a stalk 1 cm. long; the fertile segment is bipinnate on a stalk 25 mm. long; the other two fertile segments are tripinnate on stalks about 10 cm. in length. This curious plant (Fig. 13) was collected in sphagnum moss and may be a monstrosity but seems to answer to the state found by C. J. Sprague, at Hingham, Mass., as mentioned in Gray's Manual, 5th Ed. p. 672. Apparently this differs from the Sprague plant in having the long-stalked fertile segments, which represent the lateral divisions of the sterile lamina, arising from low down on the common stalk instead of at the normal positions for those divisions. Keweenaw Co., No. 627 a, July 31, 1888.

Botrychium simplex, E. Hitch.

This is a very small plant and in the field, easily overlooked. The typical form has a small, sterile frond, simple, or three-lobed, roundish, or obovate. It is usually found in low wet grounds with, or in the vicinity of, moss. Keweenaw Co., No. 3997½, July 3, 1915.

Botrychium simplex var. *angustum*, Milde.

Botrychium tenebrosum A. A. Eaton, Fern Bul., 7, 8, 1899.

This variety has a narrow, pinnate, sterile frond with 2 or 3 pairs of distant lobes. It is more frequently found in rich, moist thickets and is liable to be confused with slender and delicate plants of *B. Matricariaefolium* with which it is sometimes found in company. Keweenaw Co., No. 644 a, August 8, 1888.

Botrychium simplex var. *subcompositum*, Lasch.

The sterile lamina is pinnate with 3-5 pairs of contiguous lobes,



Figure 13. *Botrychium multifidum* var. *dichotomum*

or with the lower pair remote and narrowed to petiole-like bases. In wet, mossy fields or meadows. Keweenaw Co., No. 644, August 8, 1888.

LYCOPODIALES.

LYCOPODIACEAE.

When on the Keweenaw Peninsula in October, 1914, the season being most propitious for the work, I made a thorough study of the Club Mosses of the region. Among other things observed was the propensity of species of the section *Lepidotis* to produce prolific spikes i. e., spikes with the axes prolonged as leafy shoots; the length of the peduncles is very variable even on the same plant; sometimes the peduncle is obsolete so that the pedicles of the spikes spring from the apex of the branchlet, thus appearing as peduncles. It is customary to consider *L. dendroideum*, Michaux, as synonymous with *L. obscurum*, Linne, even though the former has terete branchlets with equal, 8 ranked leaves, while the latter has dorsiventral branchlets and unequal, 4 ranked leaves. So long as this attitude is maintained there is no excuse for keeping *L. alpinum* separate from *L. complanatum* as exactly the same conditions prevail. In the living plants of these species the tips of the leaves of the upper and lower rows of the dorsiventral branchlets are never appressed as is usually stated, in our manuals to be the case. The stems creep along the surface or at various depths down to six inches; these with the branches are always terete and bear equal 8-ranked leaves, the free portions of which are never appressed.

Lycopodium Selago, Lin var. *patens* (Beauv.) Desv.

This variety, as well as the typical species, is rather scarce on the Keweenaw Peninsula; the plant is greener than the species which is yellowish, and coarser; the leaves are narrow, more sharply pointed, and horizontal or nearly so. In wet, mossy grounds, No. 3910½. October 1, 1914.

Lycopodium clavatum, Lin. var. *megastachyon*, Fern. and Biss.

The form listed in Beal's Michigan Flora as the var. *monostachyon*, Hooker, is that plant which has more recently been described by Fernald and Bissel as *L. complanatum* var. *megastachyon*. This name should therefore be adopted for the plant found in northern Michigan, as it is very distinct from Hooker's variety.

Lycopodium obscurum, Linne.

Our local manuals describe *Lycopodium obscurum* Linne as with 6- or 8-ranked leaves with the 2 upper and 2 lower rows appressed. No plant answering to such a description could be found, and it

is very doubtful if such a plant can be found anywhere. Linne does not give the number of ranks in which the leaves are arranged but does say that the leaves are spreading (*Folia sparsa attamen varia* * * * * * *basi decurrentia s. adnata cauli, denipatula*). The only reference given by Linnaeus is "*Lycopodioides radiatum dichotomum*. Dill. musc. 274, t. 67." Dillenius' plate shows a plant that has the leaves in four ranks, the upper row being represented as now appressed and now spreading. Evidently the drawing was made from a dried plant in which naturally enough, the upper and lower leaves will most generally appear as appressed. In the living plant the leaves are four ranked on a dorsiventral axis, and ascending with incurved tips, none appressed; the free portion of the lateral leaves is about $4\frac{1}{2}$ mm. in length; of the upper, about $3\frac{1}{2}$; and of the lower, 2. The branches are dichotomously branched, the branchlets ascending with gracefully spreading, recurved tips. Foliage dark green and glossy; perhaps the most graceful and handsome of our *Lycopodiums*. Fairly well represented by the plate of Dillenius mentioned above. Stems 1 or 2 inches below the surface. Spikes 2-3 cm. Although Linnaeus said he had not seen the fructification of this species, yet, on the other hand, the Dillenian plate referred to by him shows several spikes, most of which are represented with a proliferous tip, a condition very frequently seen in this species.

Another form or variety of this species is the plant known as *Lycopodium dendroideum*, Mx. It differs much in habit; it is dichotomously branched, as in the specific type, but the branchlets are neither dorsiventral nor drooping but terete and erect, the upper being shorter, so that the plant has the exact appearance of a miniature spruce tree. The foliage is less glossy and more of a yellowish green in color, the leaves being of equal length, about $3\frac{1}{2}$ mm., and disposed in 8 ranks; the stems are 2 or 3 inches below the surface; the spikes are numerous, sessile, and from 2-5 cm. in length. This will answer very well to Michaux's description. The only reference Michaux gives is Dill. t. 64. The only American species represented on this plate is the *Selaginella apoda*. Evidently Michaux made a very poor interpretation of the Dillenian plate, if he refers to Dill. Mus. t. 64, or else the reference to it is a typographical error. I have no doubt that this form with 8-ranked, equal leaves, from its remarkable tree-like appearance which is not evident in the other forms of the species, is the plant that Michaux had in view for his *L. dendroideum* even though that author did not mention the number of ranks in

which the leaves are grouped. Most authors attribute six ranked leaves to Michaux's species but they evidently have had another variety in hand, one that is exactly intermediate between this plant and *L. obscurum*, Lin. The branchlets are erect with only the tips slightly curving outward, and are semi-dorsiventral; the leaves are unequal in six ranks, corresponding to three upper and three lower, the latter row on each side being obsolete; the lower leaves are from 2 to $3\frac{1}{2}$ mm. in length and the upper from $3\frac{1}{2}$ to 4 mm.; the middle upper row bearing the longest leaves, the middle lower row, the shortest, while the others are successively intermediate. The stems are from 4-6 inches below the surface. Spikes 2-6 cm. It may be a cross between the other two forms but it has longer spikes and the stems are deeper in the ground than in either. It may be known as *LYCOPodium obscurum*, Lin. variety *HYBRIDUM*, N. Var. The species and its synonymy is as follows:

Lycopodium obscurum Lin., Sp. Pl., 1002, 1753.

Lycopodioides radiatum dichotomum. Dill., Musc., 274, t. 67, 1741.

Lycopodium dendroideum var. *obscurum* (Lin.) Torr. ex. Beck., Botany, 460, 1833.

Keweenaw Peninsula, No. 682, September 6, 1888. In rich woods under evergreens. Frequent.

Lycopodium obscurum var. *hybridum*, Farwell.

Lycopodium Dendroideum Willd., Sp. Pl., 5, 21, 1910, and many American authors, not of Michaux.

Lycopodium obscurum Eaton & Wright, N. Amer. Bot., 309, 1840, and many American authors not of Linnaeus.

Keweenaw Peninsula, No. 3908, September 1914. Along the edge of woods and thickets. The common form.

Lycopodium obscurum var. *dendroideum* (Mx.) D. C. Eaton in Gray's Manual, 696, 1890.

Lycopodium dendroideum Mx., Fl. Bor. Amer., 2, 282, 1803.

Keweenaw Peninsula, No. 681, September 6, 1881. On knolls in the open. The rarest form.

Lycopodium complanatum, Linne.

This is a very variable species and its forms have been considered as species by those botanists who think that all variations of plants should be considered as distinct species, discarding all minor categories. This species, like *L. obscurum*, Linne, shows two well marked series; one with the leaves of equal length and in 6-8 ranks (stems not dorsiventral) and one with the leaves of unequal length and in 4 ranks (stems dorsiventral). The distinctions between

L. alpinum and *L. complanatum* are not more pronounced than those between *L. obscurum* and *L. dendroideum*, yet the former are generally considered as distinct species and the two latter as one and the same thing. As a matter of fact the distinctions are even less pronounced for *L. alpinum* shows both kinds of leaves on the same plant while the spikes of *L. complanatum* may be sessile as in *L. alpinum*. the extremes appear to be distinct enough but a complete series of intermediates connect one with the other. *L. alpinum* has priority of place in the *Species Plantarum* but since this species has been reduced to a variety of *L. complanatum*, the latter, according to Article 46 of the Vienna Rules, must be considered as the type.

Key to the varieties of L. complanatum.

Plants with dorsiventral branchlets, leaves 4 ranked, appressed—in the dried plant.

Branchlets 2-4 mm. wide, very flat, leaves unequal.

Branchlets elongated, loosely ascending.

Peduncles single, 3-12 cm., spikes 2-6—*Lycopodium complanatum*.

Peduncles, 1 or 2, 1-5 cm., spike solitary—*Lycopodium complanatum* var. *Sabinaefolium*.

Peduncles obsolete, spike solitary and sessile—*Lycopodium complanatum* var. *Pseudoalpinum*.

Branchlets short, crowded, forming funnels (fan shaped when dried).

Peduncles single, 3-6 cm., spikes 2-6—*Lycopodium complanatum* var. *flabellatum*.

Peduncles similar, spike solitary—*Lycopodium complanatum* var. *Wibbei*.

Branchlets $\frac{1}{2}$ mm. wide, biconvex, leaves nearly equal.

Leaf tips of lateral rows erect—*Lycopodium complanatum* var. *Chamaecyparissus*.

Leaf tips of lateral rows widely spreading—*Lycopodium complanatum* var. *Sharonense*.

Plants with both dorsiventral and terete branchlets, leaves 4-ranked, not appressed, spike sessile—*Lycopodium complanatum* var. *alpinum*.

Plants with terete branchlets, leaves in 5 ranks, equal, ascending, spikes solitary on peduncles less than 1 cm.—*Lycopodium complanatum* var. *Sitchense*.

The species and its more important synonyms are given below.
Lycopodium complanatum, Lin., Sp. Pl., 1104, 1753.

Stems 1-3 inches below the surface. Branchlets elongated, broad and flat, loosely ascending; peduncles 3-12 cm., carrying 2-4, occasionally more, spikes. Keweenaw Co., No. 746, July 12, 1890. Occasional.

LYCOPODIUM COMPLANATUM var. *SABINAEFOLIUM* (Willd.), N. Comb.

Lycopodium Sabinaefolium Willd., Sp. Pl., 5, 20, 1910.

Lycopodium alpinum var. *Sabinaefolium* (Willd.) D. C. E. in Gray's Man., 696, 1890.

Free portion of leaves longer and narrower, peduncles shorter, solitary, or in twos, spikes solitary, upper leaves often in two rows, the leaves then being 5-ranked, a transition toward var. *Sitchense*. Stems an inch or so below the surface. Keweenaw Co., No. 746½, July 12, 1890. Rare.

Lycopodium complanatum var. *flabellatum*, Döll, Fl. Bad., 1, 79, 1855.

Lycopodium anceps Wallr. Linnea, 12, 676, 1840.

Lycopodium complanatum var. *anceps* Aschers., Fl. v. Brand, 1, 894, 1864.

Lycopodium complanatum var. *flabelliforme* Fernald, Rhodora, 3, 280, 1901.

Lycopodium flabelliforme (Fernald) Blanchard, Rhodora, 13, 168, 1911.

This variety is very readily detected in the field by its foliage being arranged in the form of funnels and in herbarium materials by its short, fan-shaped clusters of branches arranged in distinct series one above another. Its stems are above ground. Keweenaw Co., No. 1785 and 1785½, August, 1902; No. 3911 and 3912 (proliferous form), October, 1914.

Lycopodium complanatum var. *Chamaecyparissus* (A. Br.) Döll, Fl. Bad., 1, 80, 1855.

Lycopodium tristachyum Pursh, Fl. Am. Sept., 653, 1814.

Lycopodium Chamaecyparissus A. Br. ex. Mutel, Fl. Fran., 4, 192, 1837.

Lycopodium complanatum var. *Sabinaefolium* (Willd.), A. Gr., Man., 674, 1867.

The most glaucous form, with the narrowest branchlets, longest peduncles, and most numerous spikes. The commonest form on the Keweenaw Peninsula. Stems 5-6 inches under the surface. No. 686. Sept. 10, 1888.

LYCOPodium COMPLANATUM var. SHARONENSE (S. F. Blake), N. Comb.

Lycopodium tristachyum var. *Sharonense* S. F. Blake, Fern Bull., 18, 9-10, 1910.

Similar to the preceding but the free portion of the leaves are spreading or recurved. Keweenaw Peninsula, No. 746 a, July 12, 1890. Rare.

Lycopodium complanatum var. *alpinum* (Lin.), Spring, Flora, 1, 180, 1838.

Lycopodium alpinum Lin., Sp. Pl., 1104, 1753.

The stems are close to the surface; leaves unequal, ascending, in 4 ranks; spikes sessile. Keweenaw Peninsula, No. 849, June 30, 1895. Rare.

Three other varieties may be confidentially looked for. These are: var. *Wibbei*, Harberer, which is similar to the var. *flabellatum* but with the spike solitary; LYCOPodium COMPLANATUM var. PSEUDOALPINUM, N. var., briefly described as like the specific type but with sessile spikes, a transition toward the var. *alpinum*; and LYCOPodium COMPLANATUM var. SITCHENSE (Rupr.), N. Comb. (*Lycopodium Sitchense* Rupr., Beitr. Pfl. Russ, Reich., 3, 30, 1845). Variety *Pseudoalpinum* is well represented by plate 233, Journal of Botany, Vol. 20, 1882.

Department of Botany, Parke, Davis & Co., Detroit, Mich.

A CONVENIENT METHOD OF WASHING FIXED PREPARATIONS.

BY RICHARD DE ZEEUW.

It is comparatively easy to wash a limited amount of material after fixation, but when it comes to taking care of the washing of material for a large class in technique, cytology or embryology, the instructor in charge is faced by a rather annoying problem. The objection to all the schemes suggested is in the fact that the sink, which above all else should be kept free, is all cluttered up.

The writer has constructed a bit of apparatus, which has given very satisfactory service for two years. It has appealed to all who have seen it as answering the purpose admirably. That is the excuse for the present note.

The apparatus (Fig. 14) consists of a galvanized iron box (A), which may be made of any required dimensions. There is a pipe (B) to enable one to have a constant stream of water running in the trough, which has an overflow pipe (C) at the opposite end. The material to be washed is put in Gooch Crucibles. A piece of cheese-cloth is put over the opening, and a rubber band is snapped around it to keep the cheese-cloth in position. The whole is then immersed in water bottom side up. The bottom of the crucible is perforated with small holes. The air is thus allowed to escape and the water to enter the crucible. Care should be taken not to immerse it so far as to cause the water to close up the openings. This will keep that air in, when the crucible drops to the bottom of the trough on being released the air is out. If not, take it out, blow in the holes to free them of water and try again.

The crucibles may have a thread run through one of the holes and a tag fastened to the other end, which hangs on the outside of the trough. This enables any one to remove any particular specimen from the wash-trough without disturbing any of the others.

Since there is a continual current of water in the trough, it has been found advantageous to place the crucibles on their sides with the ends directed toward the ends of the trough. Thus the current will pass in at the cheese-cloth covered end and out at the perforated end ensuring perfect removal of the fixing agent. And,

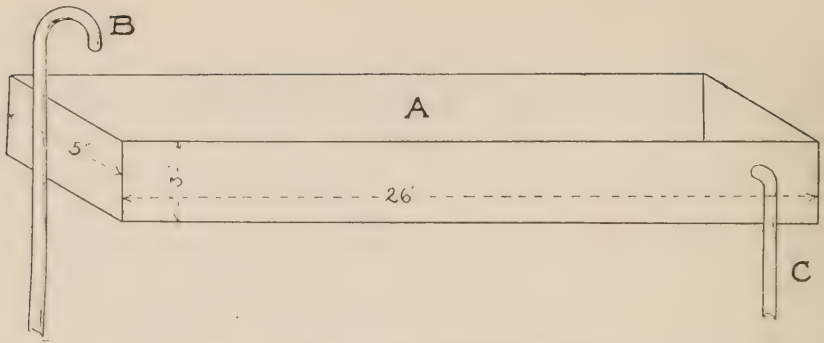


Figure 14. Tank for washing fixed preparations.

since the current is so gentle, no damage has ever been done to the most delicate material.

The whole apparatus may very conveniently be placed on a shelf over or near the sink.

Michigan Agricultural College, East Lansing, Mich.

ZOOLOGY.

NOTES ON PLEODORINA CALIFORNICA SHAW.

BY BERTRAM G. SMITH.

On July 23, 1915, the writer found the colonial flagellate *Pleodorina californica* Shaw in great abundance in a pond near White's Woods, Ann Arbor, Michigan. *Pleodorina* was most plentiful at the margin of the pond, where by pressing down the mat of vegetation hollows were formed which soon filled with water. In a vial of this water held to the light, *Pleodorina* was barely visible to the naked eye. When the material was placed in a finger bowl in the laboratory, exposed to the light of a north window, the specimens sought the side of the dish furthest from the light—a case of negative phototaxis that seems remarkable in view of the behavior of *Euglena* and *Volvox* in similar circumstances. Such a reaction in a chlorophyll-bearing flagellate would seem almost suicidal. Specimens undergoing reproduction became less motile and sank to the bottom of the dish. The material does not live long in the laboratory. Ten days later, it had completely disappeared from the pond. The occurrence of *Pleodorina* has been noted in California, where it was first discovered, also in Illinois, Indiana and in southern France; I am not aware of any previous record for Michigan.

Pleodorina is a colonial protozoan, each specimen in the adult stage consisting of typically 128 greenish bi-flagellate cells enclosed in a common gelatinous envelope and loosely arranged to form a hollow sphere. There is a decided difference in the size of the cells on opposite sides of the colony. On one side, comprising a little less than a hemisphere, the cells are quite small; these are the somatic or body cells. On the other side, comprising a little more than a hemisphere, the cells are much larger; these are the reproductive or germ cells. The form of the colony is not exactly spherical, but is usually elongated slightly in the direction of the axis of radial symmetry; in other words the colony has the form of a prolate spheroid, with the body cells segregated about one pole. Since the end composed of body cells usually precedes in locomotion, this end may be called the anterior end and the opposite end the posterior end.

Both body and germ cells have each their own individual gelatinous envelopes, which may be made out by careful manipulation of the high power of the microscope. Each kind of cell has two flagella projecting through the common gelatinous envelope. Each cell has a red eye-spot and numerous green chloroplasts.

Reproduction takes place asexually by the repeated division of the germ cells or parthenogonidia to form daughter colonies. A complete series of developmental stages comprises 2, 4, 8, 16, 32, and 64 cell stages. The daughter colonies eventually break out from the enclosing parental envelope. At the time of its escape each daughter colony consists of either 64 or 128 cells all of the same size; the germ cells are later differentiated by an increase in size. At the time of the escape of the daughter colonies, the body cells of the parent degenerate and die.

Though *Pleodorina* is undoubtedly a protozoan colony, it is in some respects transitional to the metazoa and for purposes of comparison with the metazoa it may be regarded as an individual organism. *Pleodorina* is the simplest and most primitive organism showing a separation or segregation of body cells from reproductive cells; in other words, it is the simplest organism showing differentiation of structure and division of labor between somatic and germ cells. It is also the simplest organism which clearly undergoes natural death; but it is only the body cells which die, while the germ cells live to give rise to a new generation of bodies and germ cells. In *Pleodorina* the fundamental biological principles of segregation of the body plasm and continuity of the germ plasm are exemplified in their simplest form, without the complication of sexual reproduction such as is found in *Volvox*.

The value of such a type for elementary classes in biology is obvious. *Pleodorina* readily falls in place in the series leading from the simplest colonial flagellates, such as *Gonium* and *Pandorina*, to *Volvox*. Unfortunately *Pleodorina* is of rather exceptional occurrence, but since when found at all it is likely to be present in abundance, a supply sufficient for several years may be preserved. Material fixed in weak Flemming's solution (one part of strong Flemming to three parts water) for twenty-four hours, then thoroughly washed and preserved in 5% formalin, retains the natural appearance and form of the colony, and for class use is almost as good as fresh material. The writer has prepared *Volvox* in this way and found it in good condition for about six years, after which the finer details of structure were lost.

Zoological Laboratory, State Normal College, Ypsilanti, Mich.

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THE PROCESS OF OVULATION IN AMPHIBIA.

BERTRAM G. SMITH.

In all vertebrates, there is discontinuity between the ovaries and the ducts which convey the eggs to the exterior—a lack of adaptation which becomes intelligible only in the light of studies concerned with the origin and evolution of the coelomic cavity. In the higher vertebrates, the approximation of the funnel-shaped inner end of the oviduct to the ovary safeguards to a considerable extent the passage of the eggs into their proper channel; but in the amphibia the two organs are widely separated, and the problem of how the eggs find their way into the oviduct has been a puzzling one. As a result of some observations on *Cryptobranchus* and *Rana pipiens*, I have become convinced that the generally-accepted explanation of this process is incorrect. In connection with this study some observations of minor importance were made on the escape of the eggs from the ovary of *Cryptobranchus*.

1. *The escape of the eggs from the ovary.* Judging from the published accounts, direct observations on the escape of the amphibian egg from the ovary are rare. Brandt ('76) examined the outer surface of the ovary of *Rana temporaria* as the eggs were about to pass into the body cavity and found a small round hole above each egg through which a larger or smaller part of the egg protruded. Recently I have observed various stages of the process in several different adult females of *Cryptobranchus* which had been killed by pithing and the body cavity immediately opened.

A very small portion of the egg first protrudes as a minute spherical exovate connected by a very narrow stalk with the remainder of the egg which is still covered by the ovarian wall and follicle. Very slowly the exovate becomes larger. Under the conditions noted the process has not been observed to go very far; perhaps the pressure of surrounding parts on the ovary, and especially the movements of the viscera during locomotion, are normally required to complete the expulsion of the egg. But slight pressure with an instrument on the portion of the egg still in the ovary completes the process as follows: The exovate increases in size until it equals the part of the egg still in the ovary; at this time the egg is shaped like an hour-glass. Then the enclosed part of the egg flows out with remarkable suddenness, and the entire

egg immediately rounds up into an oblate spheroid, considerably flatter than the egg at the time of spawning.

At the time when the egg is half-way out of the ovary it is constricted to a remarkable degree: the stalk connecting the two halves of the egg is scarcely more than 2 millimeters in diameter, while the diameter of the entire egg after it assumes the spherical form exceeds 6 millimeters. The plasticity of the egg at this time contrasts strongly with its condition during early cleavage. In the first cleavage stage I attempted to separate the first two blastomeres by tying a silk thread around the egg in the plane of the first cleavage furrow; the egg would not bear a constriction of more than 2 millimeters, leaving the constricted portion more than 4 millimeters in diameter. The greater plasticity of the ovarian egg seems to be due to a lesser degree of turgor, or tension of the egg membrane; perhaps the egg later absorbs water.

As in *Bufo* (King, '02), the egg doubtless escapes through the stalk of the follicle, since here the egg is enclosed by only two cellular membranes, elsewhere by three. Since only a small proportion of the eggs are found escaping from the ovary at any given time, the liberation of all the ripe eggs must require a considerable period of time, probably several days.

2. *The passage of the eggs down the oviduct.* In *Cryptobranchus*, peristalsis of the uterus and the lower oviduct was observed, but none in the upper oviduct. An egg placed in the funnel of the oviduct of a prostrate specimen moved down the oviduct very slowly. At the end of an hour it had moved 2 centimeters further than the position to which it may have been carried by gravity. I scraped the lining of the upper oviduct and examined the scrapings under the microscope; the epithelial cells possessed cilia. One can only conjecture whether the ciliary action in the oviduct is strong enough to carry the eggs along; possibly it is aided by peristaltic action too slow to be observed.

3. *How do the eggs get into the oviduct?* Newport ('51) believed that, owing to the close attachment of the oviducts at their inner openings to the walls of the pericardium, at each contraction of the heart the slit-like openings of the oviducts would gape open, and any eggs in the vicinity might be forced, by suction, into the mouths of the tubes. Also, he thought that owing to the muscular movements of the body, and the resultant shifting of the internal organs, the eggs sooner or later pass near the openings of the oviducts, and are then carried into the tube. According to Nussbaum ('95) the eggs, when set free from the ovary into the

body cavity of the frog, are carried into the open mouths of the oviducts by the motion of cilia of the coelomic epithelium; these cilia drive anteriorly any solid objects lying free in the body cavity. He states that the cilia are not uniformly distributed, but occur in patches on the peritoneum of the body wall and mesentery. Nussbaum's version of the matter has been quite generally accepted.

In order to test the validity of Nussbaum's conclusions I took several female specimens of *Rana pipiens* during the breeding season when the eggs were still in the ovary, and tested the mesentery and other parts of the peritoneum for ciliary action, using powdered carmine, blood and cork filings. There was absolutely no evidence of ciliary action. As a check on this experiment I used the same means to detect ciliary action on the roof of the mouth cavity and oesophagus of the same frogs, and obtained the most lively evidence of ciliary motion. In like manner I have thoroughly tested the peritoneum of female specimens of *Cryptobranchus* during their breeding season, with absolutely negative results. In both *Rana pipiens* and *Cryptobranchus*, I scraped the peritoneum in various parts of the body cavity and by examining the scrapings under the microscope found indeed that there were occasional patches of cilia, but the foregoing experiments indicate that in *Cryptobranchus* and in *Rana pipiens* ciliary action is not powerful enough to carry along foreign particles to any appreciable extent, and certainly not strong enough to move the large and heavy eggs. In the absence of sufficient ciliary action, we must look for mechanical factors to insure the transmission of eggs to the oviduct. My observations and experiments have convinced me that Newport's views, and not Nussbaum's, were essentially correct, at least when we attempt to apply them to the species under consideration. The following conclusions were written by me before I was aware of Newport's theory.

The funnel is so placed as to open in an anterior direction. Eggs that by any chance get into it cannot easily get out by retrogressive movements, since they are pressed upon by other eggs and are soon carried down the oviduct. Thus the funnel acts as a trap to catch eggs. At the beginning of the process some eggs lying free in the body cavity must get into the funnel by chance, aided by the muscular movements of the animal which keep them in circulation. These eggs are carried down the oviduct and collect in the uterus. Since the uterus is located at the posterior end of the body cavity while the funnel is at the anterior end, the pressure of the increasing mass of eggs in the uterus must force the eggs

remaining in the body cavity forward. Thus there is an increasing tendency for them to get into the funnel.

If this interpretation is correct, one would expect that occasionally a few eggs would be left permanently in the body cavity; such a mechanism could not be expected to work with absolute perfection. Observation shows that this is what actually occurs. In many specimens of *Cryptobranchus*, after spawning, a few eggs are still to be found in the body cavity; if the animals were allowed to live these eggs would probably later be absorbed. On the other hand, if eggs were carried into the oviducts by ciliary action, one would expect that none would be left behind.

In examining Newport's extensive contributions on the early development of the amphibia, one cannot fail to be impressed by his masterly analysis of the problems of embryology and by the pioneer character of his work. With almost prophetic insight he has laid the foundations of much of the "experimental embryology" of a later generation.

Zoological Laboratory, State Normal College, Ypsilanti, Mich.

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BIBLIOGRAPHY

OF

PERIODICAL LITERATURE AND PUBLICATIONS OF LEARNED SOCIETIES OF
INTEREST TO ZOOLOGISTS IN THE UNIVERSITY OF
MICHIGAN LIBRARY.

COMPILED BY ROBERT W. HEGNER.*

This list has been prepared for the following purposes:

(1) To collect and arrange titles of all periodical literature in the library of interest to zoologists in such a manner that it will be possible to determine quickly whether we have or do not have any particular volume or number.

(2) To provide an easy method of finding reports by publishing the library call numbers.

(3) To make it possible to determine the needs of the library with regard to periodicals of this character. (Any suggestions from those interested will be appreciated.)

(4) To aid scientists throughout the State of Michigan by publishing a list which will inform them as to the available zoological literature in the library.

Periodical literature and the publications of the learned societies are classified in the University of Michigan Library according to Dewey's Decimal System.

The publications of learned societies are in the upper reading room of the general library. They are placed on the shelves according to (1) the country or language (American, English, German, French, Italian, etc.), (2) the city in which they were published, and (3) the initial of the first word of the official title.

Other periodical literature will be found in the stacks of the general library or in one of the branch libraries on the campus as indicated in the appended summary of classification. The official publications of societies are placed either under the name of the society, e. g., the Biological Bulletin under the name Marine Biological Laboratory, or under the title of the publications, e. g., the official organ of the Audubon Societies under Bird Lore. Printed directories giving the position of periodicals according to call num-

*The writer is indebted to Miss Grace Powers of the Zoology Department and to several members of the library staff for assistance in preparing this report.

bers will be found posted in the stacks of the general library.

The branch libraries that may contain periodicals of interest to zoologists are as follows:

- (1) Natural Science Library in the Natural Science Building;
- (2) Histological Library in the Medical Building;
- (3) Hygienic Library in the Medical Building;
- (4) Chemical Library in the Chemistry Building;
- (5) Russell Library in the Natural Science Building.

Most of the current periodicals are placed in the natural science library, in the periodical room of the general library or in the medical periodical room in the General Library, although certain publications are put directly in the stacks.

Number.	Name.	Volume.	Year.
506.1A3316t.....	Albany Institute. Transactions.....	1-12	1830-1893
590.5A43F5.....	Allgemeine fischereizeitung.....	31-40	1906-1915
506.1A5A85p.....	American Association for the Advancement of Science. Proceedings.....	1-62	1848-1911
630.5A5B84.....	American Breeder's Magazine. Washington	1-4	1910-1913
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610.5A5J86A5.....	American Journal of Anatomy.....	1-19	1901-1916
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505A5J9S4.....	American Journal of Science.....	1-190	1818-1916
610.5A5J86T77.....	American Journal of Tropical Diseases.....	2-3 (incomp.)	1915-1916
570.5A5M179M16.....	American Monthly Microscopical Journal..	1-23	1870-1902
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570.5A595B6.....	Annales de Biologie Lacustre, Bruxelles.....	1-6	1906-1913
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570.5A.....	Annals and Magazine of Natural History...	2nd Ser. v. 19 8th Ser. v. 16	1857-1915
578.5A595M6.....	Annales de Micrographie.....	1-10	1888-1898
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590.5N67.....	Niederlaendisches Archiv für Zoologie.....	1-5	1871-1882
610.5A67P57M6.....	Archiv für die gesammte Physiologie. Pflüger	1-162	1868-1915
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610.5A671I9.....	Archives Italiennes de Biologie.....	1-63	1882-1915
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506.4B72S6.....	Bordeaux. Societe des Sciences physiques et naturelle. Memoires.....	Series 1, 2, 3, 4, 5, 6, 1-7	1854-1908
570.5B.....	Boston Journal of Natural History.....	1-7	1834-1963
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506.2C18P5t.....	Cambridge Philosophical Society. Transac- tions.....	1-22	1822-1915
595.75C2E6.....	Canadian Entomologist.....	1-48	1869-1916
506.2C24S7r.....	Cape Town. South African Association for the Advancement of Science Report.....	1-6	1903-1909
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506.1C2916y.....	Carnegie Institution of Washington. Year- book.....	1-14 1-29	1902-1915 1884-1913
591.05C39.....	LaCellule.....	1-76	1887-1915
616.05C4B2.....	Centralblatt für Bakteriologie.....		
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570.5C48b.....	Charleston Museum Bulletin.....	2-12	1906-1916
506.4C52S68m....	Cherbourg. Société nationale des sciences naturelles et mathématiques. Mémoires.....	36-38	1906-1912
570.5C57S7j.....	Cincinnati Society of Natural History. Journal.....	1-21	1878-1914
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506.1C72U6s.....	Colorado University Studies.....	1-11	1902-1915
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506.2D8R9p.....	Dublin Royal Irish Academy Proceedings....	1-32	1836-1915
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